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STUDIES IN THE ANATOMY OF FERNS

A thesis submitted to the University of Glasgow,
for the degree of Doctor of Philosophy
in the Faculty of Science

by

Udayananda Sen, M.Sc.

April, 1961

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PREFACE

This thesis is a study of the anatomy of certain ferns. It has been divided into two parts, the first dealing with the anatomy and the phylogenetic relationships of the tree ferns and their allies, and the second, with the anatomy and distribution of Ophioglossum reticulatum L.

Acknowledgements

I would like to express my sincere thanks to Professor John Walton for placing at my disposal the facilities of the Botany Department at Glasgow University for the purpose of these studies. I should also like to thank him for his kindly interest, helpful suggestions and constructive criticisms made during the course of the investigations.

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Professor H.J. Lam, Dr. C.D. Adams, Mr. E. Curtis, Dr. M.B. Raizada, and Dr. K.U. Kramer, also the Director, Botanic Garden, Kew, all provided material for the study and I should like to thank them for their assistance. I am indebted to Mr. W. Anderson who was responsible for most of the photographs, and also to Mr. W. Jack for much assistance.

This work was carried out while on the staff of the City College (Calcutta University) and I thank the authorities of this College for granting me study leave and other facilities.

PART I

STUDIES IN THE ANATOMY OF TREE FERNS AND THEIR ALLIES

INTRODUCTION

The genera mainly concerned are those included by Diels (1902), in the single family Cyatheaceae, i.e. Balantium (= Culcita), Dicksonia, Cibotium, Thyrsopteris, Cyathea, Hemitelia and Alsophila. They are usually confined to the tropics and subtropics, but some grow in temperate regions, especially in the southern hemisphere. These plants are chiefly inhabitants of húmid forests, although some are xerophytic and grow luxuriantly in open places freely exposed to the sun. They are truly the giants of the fern race, though all are not dendroid in habit; some are even creeping.

The fronds are large and usually much dissected, but in certain genera the 2-pinnate or even 1-pinnate conditions are very common. In extreme cases the fronds may be entire. The veins of the fronds are usually free, but in some cases they may be anastomosing. The surface of the stem, at least in the younger regions, and the bases of the petioles are covered either only with hairs or by both hairs and scales. The sori, which are globose or oblong, are either marginal or abaxial in position, and usually gradate. The indusia show a wide variation of form: they may be two-lipped, saucer like, cup-shaped, vestigial, or absent. The sporangia, which dehisce transversely by an obliquely vertical annulus, may be almost sessile or stalked. The cordate gametophyte at maturity may have a conspicuous midrib, and the archegonia are of the usual type. The antheridia, however, are complex and their walls consist of five cells. Such are the main characteristics of the seven

genera.

Diels grouped the genera into three Tribes according to the position of the sori and the shape of the indusium. The seven genera were characterised according to the following scheme:

A. Sori on the tips of fertile veins. Indusium extrorse, beaker-like, formed from the more or less modified tip of the leaf-margin. Rim of the sporangium with a stomium of thinner cells..... I. Dicksonieae.

(i). Fertile leaflet hardly modified. Indusium two-lipped, leathery.

a. Pinna segments of the last order strongly asymmetrical. Stem hardly raised above the ground..... 1. Balantium.

b. Pinna segments of the last order almost asymmetrical. Stem upright... 2. Dicksonia.

(ii). Fertile segment lobe strongly modified, and similar to the indusium.
Indusium two-lipped..... 3. Cibotium.

B. Sori on the tips of fertile veins, indusium inferior, finally hemispherical. Rim of the sporangium with cells of the same kind..... II. Thyrsopterideae.
4. Thyrsopteris.

C. Sori on the backs or in the bifurcations of fertile veins. Indusium inferior, spherical, to beaker shaped, very often more or less irregularly torn, or scale-like or absent. Rim of the sporangium of almost similar cells. Stomium only slightly differentiated
..... III. Cyatheeae.

(i). Sorus with membranous, dish-shaped, smooth margined, or at first spherical closed, and later irregularly torn indusium
..... 5. Cyathea.

(ii). Sorus with membranous, incomplete scale-like indusium..... 6. Hemitelia.

(iii). Sorus without indusium..... 7. Alsophila.

Prior to Diels, these seven genera had received very varied treatment at the hands of taxonomists.

Presl (1836), placed Cyathea, Hemitelia and Alsophila in the Tribe Cyatheaceae of the Sub-order Helicogyratae. Thyrsopteris and Cibotium were grouped with Peranema under the Tribe Peranemaceae, while Balantium, Dicksonia and Culcita were placed in the Tribe Dicksoniaceae, both Tribes being in the Sub-order Cathetogyratae.

J. Smith (1841), placed Dicksonia, and Cibotium along with Sitobolium (Dennstaedtia) in Dicksoniae, section 4 of the Tribe Dicksonieae. Cyathea, Hemitelia and Trichopteris (Alsophila) were placed in the Tribe Cyatheae.

Fee (1852) grouped Dicksonia with Hypodorris, Woodsia, etc. and placed them in Dicksonieae, Balantium along with Leptopleuria and Cystodium under Balantieae, Cibotium under Cibotieae, Alsophila, Hemitelia, Amphidesmia, etc. in Cyatheae, and Thyrsopteris under Thyrsopteridieae.

Moore (1857), placed Dicksonia, Dennstaedtia, etc. in the Tribe Polypodineae, while Thyrsopteris, Cyathea, Hemitelia, Amphicosma, Alsophylae, Amphidesmium were placed in the Tribe Cyatheineae.

In the Synopsis Filicum of Hooker and Baker (1874), Cyathea, Thyrsopteris, Hemitelia, Alsophila, Diacalpe, and Matonia constitute the Tribe Cyatheae of the Polypodiaceae, while Dicksonia, Woodsia, Onoclea, etc. are placed in the Tribe Dicksonieae.

Sodiro (1893), placed Cyathea, Hemitelia, and Alsophila in Cyatheaceae, and Dicksonia, Woodsia, etc. in Polypodiaceae.

Christ (1897), placed Dicksonia, Cibotium, Cyathea,

Alsophila, Hemitelia, and Thyrsopteris in the family Cyatheaceae, but did not recognize Balantium as a distinct form.

Raciborski (1898), included Cyathea, Hemitelia, and Alsophila under Cyatheaceae, but placed Dicksonia under Polypodiaceae.

Progress in the taxonomy of these plants in the period following Presl's work was slow. This was due to the fact that during this period the grouping of ferns was based mainly on the characters of the sori, sporangia and the indusia, venation of the fronds, whether the fronds were adherent or articulated with the rhizome. With the acceptance of the theory of evolution as a basis for systematic work, Christ (1897) made the first successful attempt, mentioned above, to group these ferns under the Cyatheaceae, after studying the characters of the whole plant.

Both Diels and, a little later, Christensen (1906) included Balantium (=Culcita), Dicksonia, Cibotium, Thyrsopteris, Cyathea, Hemitelia, and Alsophila in a single family, the Cyatheaceae. This arrangement was widely accepted for a considerable period. It was, however, strongly criticised by Bower, who, in his Filicales, vol. II, divided the Cyatheaceae as recognised by Diels and Christensen into two families, the Dicksoniaceae, and the Cyatheaceae. He sub-divided the Dicksoniaceae into three Sub-families: i. Thyrsopteridoae (Thyrsopteris); ii. Dicksonieae (Balantium, Dicksonia and Cibotium); and iii. Dennstaedtiinae (Dennstaedtia, Microlepia, Leptolepia, Saccoloma and Hypolepis). Three genera only - Cyathea, Alsophila and Hemitelia - were placed in the Cyatheaceae.

The evidence on which this separation of the Dicksoniaceae from the Cyatheaceae is based is outlined by Bower (loc. cit., p.236). The greatest weight is placed on

the position of the sorus, a feature which had led him to recognise two distinct phyletic lines in the ferns at large. These were the Marginales (with marginal sori) and the Superficiales (with superficial sori). The former series led from the Schizaeaceae to the Dicksoniaceae; the latter from the Gleicheniaceae through the Protocyatheaceae to the Cyatheaceae. Other constant differences between the Dicksoniaceae and the Cyatheaceae, such as occur in the general anatomy, and dermal appendages, are also stressed and Bower concludes that "The difference leaves little doubt of the propriety of separating the Dicksoniaceae from the Cyatheaceae".

Christensen's later scheme of classification (1938) follows that of Bower in recognising the Dicksoniaceae and the Cyatheaceae as separate families. His Sub-division of the Dicksoniaceae is, however, different, only two Sub-families being recognised - the Thyrsopteroideae (Thyrsopteris) and the Dicksonioideae (Dicksonia, Cibotium, Culcita (?), and Cystodium (?)). The content of the Cyatheaceae remains as in Bower's scheme.

Copeland (1947), did not recognise the family Dicksoniaceae. He included Thyrsopteris, Dicksonia, Cibotium, Culcita in the family Pteridaceae, an extensive family including also the Dennstaedtia, Lindsaya, and Pteris groups and all the Gymnogrammoids. He recognised seven genera - Lophosoria, Amphidesmium (= Metaxya), Cyathea, Trichopteris, Cnemidaria, Gymnosphera, and Schizocaena in Cyatheaceae.

Holttum (1949), supported broadly the systematic scheme of Bower, and derived the Dicksoniaceae from the primitive Marginales, though not through the Schizaeaceae, while Cyatheaceae was derived from the primitive Superficiales through Gleicheniaceae. He recognised Dicksonia, Cibotium,

Cystodium, and Thyrsopteris under Dicksoniaceae, but placed Culcita in the family Dennstaedtiaceae. He did not mention any genera under Cyatheaceae, and wrote, "It was formerly the custom to recognise genera based on presence or absence of an indusium but these genera are artificial. Groups of species based on other characters (scales, etc.) have for the most part not yet been successfully established". He expressed the view that much more information is needed to establish a really phyletic scheme. He thought that some factors not mentioned by Bower may be important in phyletic schemes, and further that different sets of factors may be the significant ones in different groups of ferns.

Holttum (1957) accepted the Cyatheaceae as delimited by Copeland (but excluding Lophosoria and Amphidesmia) as a natural family. He maintained, however, his objections to the generic groupings suggested by Copeland and most earlier workers, regarding the criteria used as unsatisfactory. He suggested that such generic groupings should be replaced by a division of the family into two groups, possibly Sub-genera of Cyathea, on the basis of scale characters. Species with setiferous scales (fig. 5) should be placed in the Sphaeropteris group, those with flabelloid scales (fig. 54) in the Gymnosphaera group.

It may be noted that neither of the two new families of Bower have remained stable. The two genera of Protocyatheaceae, Lophosoria, and Amphidesmia, have been returned to the Cyatheaceae in some of the later classifications, but Dicksonia, Cibotium, Culcita, and Thyrsopteris, which have been separated from the Cyatheaceae as members of the Dicksoniaceae have never been returned to it. The authors who do not accept Dicksoniaceae, as delimited by Bower, either in whole or in part, unite one or more of the component genera with genera from the

Polypodiaceae, sens. lat. in one of the newer families.

The above brief outline of the systematic vicissitudes of the forms associated with Dicksonia on the one hand and those associated with Cyathea on the other, will serve to indicate the difficulty of the problems raised. There is first the broad problem relating to the relationship between the Dicksoniaceae and the Cyatheaceae. As shown above, the earlier systematists recognised these as separate families. Then followed a period when Diel's view, that all the genera involved could be placed in the single family Cyatheaceae, was widely accepted. Following Bower, however, all recent writers have reverted to the earlier view that the Dicksonia and Cyathea groups have developed along widely separated evolutionary lines. Recently, however, Professor Holttum told the writer that his morphological studies indicate the possibility that the Dicksoniaceae and Cyatheaceae are more closely related than Bower thought.

A second problem relates to the generic groupings within the family of the Cyatheaceae, sens. st.. As Holttum has indicated, there is as yet no satisfactory answer to this problem.

The anatomical investigations described in this part of the thesis have been undertaken to provide data which may be of use in resolving these and other problems raised by the tree ferns and their allies.

Historical Review of Anatomical Works on Cyatheaceae.

Although Hooke and Grew laid the foundation of plant anatomy in the seventeenth century, it is not until the early part of the eighteenth century that any notable contributions to the anatomy of tree ferns are found in the literature.

The first important work on the subject is that of Link (1826), who reported the presence of a discontinuous ring of wood ensheathed by brown tissue in the stems of the tree ferns of Brazil.

Von Mohl (1833) gave a fuller account of the anatomy of the stems of Cyathea and Alsophila. He noted the outer protective layers consisting of inner fibrous and outer parenchymatous cells, the stele with V- or W-shaped meristeles, the presence of small medullary bundles, the characteristic arrangement of the traces in the petiole and the connection of the internal petiolar strands with the medullary strands.

A radial dictyostelic condition in the stems of Cyathea aurea, Alsophila microphylla, and A. quadripinnata (= Lophosoria) was reported by Karsten (1847). The leaf-trace is simple in Alsophila quadripinnata, but in the others it is divided.

Nördlinger (1859), stated that in Balantium karstenianum the stem has a radial dictyostele. He found a similar condition with internal strands in Hemitelia integrifolia.

Reichardt (1859), found that the stems of Alsophila villosa, A. aspera, Hemitelia multiflora, Cyathea mexicana, and C. obonina are dictyostelic. He noticed additional cortical bundles in Alsophila armata and A. caracasana.

Mettenius (1864) stated that in the stems of Dicksonia antarctica, D. karstenlana, Cibotium schiedei,

C. glaucescens (C. barometz) the wavy vascular bundles are arranged in a ring. The margins of these bundles are curved outward. In Hemitelia, Alsophila, and Cyathea in addition to the wavy bundles, which are surrounded by brown tissue, there are small bundles in the pith. These bundles are sometimes accompanied wbyh brown tissue. However, in Alsophila pruinata (= Lophosoria pruinata) and A. blechnoides (= Metaxya rostrata), which are solenostelic, no medullary bundles are present. The numerous vascular bundles in the petioles of Cyathea arborea, Hemitelia capensis, and Alsophila radens are arranged in a characteristic manner, and some of the inner bundles pass through the leaf-gap into the pith, and anastomose with one another.

Russow (1872), reported the presence of gum canals and tannin canals in the cortex of cyathean stems.

Scott (1874), in his notes on the tree ferns of British Sikkim, gave a superficial account of the stem of Cyathea spinulosa, Hemitelia decipiens, Alsophila latebrosa, A. contaminans, A. ornata, A. comosa, A. andersonii, and A. glabra.

In his Comparative Anatomy of the Phanerogams and Ferns, de Bary (1877) referred to the previous work, notably to that by Mettenius, and also incorporated his own observations. In Dicksonia antarctica, Dicksonia karstoniana, Cibotium schiedei, C. glaucescens, Alsophila pruinata, and A. blechnoides the vascular tissue is a fluted cylinder, perforated by foliar gaps into a variable number of meristeles, the margins of which are curved outwards. In the majority of the species of Cyathea and Alsophila, in addition to the fluted cylinder, which is covered by a brown tissue, numerous small medullary bundles are found. These medullary bundles originate from the foliar gaps and form a delicate network in the pith, while some of them pass into

the petiole. Accompanying the medullary bundles are sclerenchymatous sheaths, which may themselves form a tough network. In some species (e.g. Cyathea imrayana) accessory cortical bundles are also present. In the petiole the vascular strands are arranged in a characteristic manner.

The stem structure of Alsophila palaeolata was described by Lachman (1889). In this species numerous cortical bundles, which form a network, are not connected to the stele but to the leaf traces. Traces to the numerous roots are also inserted on the cortical strands. He also described the stem structure of Dicksonia squarrosa.

Diels (1902), while describing the morphology of the Cyatheaceae, also took into account their anatomical characters.

By the beginning of the century, therefore, the main anatomical features of the tree ferns had been investigated in a general way. In the period since then, the work of a few investigators has greatly extended our knowledge of these plants. Bower in particular made many important contributions which need not be detailed here since all the main points are clearly set out in Vol. 2 of The Ferns (1926). Gwynne-Vaughan (1903) had already worked out the anatomy of Cibotium barometz and the ontogeny of the vascular system of Alsophila excelsa. Other contributions made in the period 1900 - 1926 may be briefly mentioned. In 1906, Schutze recorded the presence of "false sieve tubes" (or tangential cells, as they are now called) in the meristeles of some tree ferns and also the association of excretory cells with the phloem. The development of young plants of Cyathea and Dicksonia was described by Stephenson in 1907. In 1908, McNicol described the cavity parenchyma which is associated with the protoxylem region in the petiolar traces of Alsophila excelsa, Dicksonia antarctica and Cibotium barometz.

The pinna traces of a number of tree ferns were described by Davie in 1918. Williams (1925) described some features of the anatomy of Dicksonia antarctica and D. squarrosa.

The most important additions to our knowledge of tree fern anatomy in the period following the publication of Bower's Vol.2 of The Ferns were made by Ogura. In papers published in 1927 and 1930 he described the anatomical structure of a number of Japanese tree ferns and gave a key based on this for their specific determination. Ogura (1927) also described the anatomy of two mesozoic tree ferns, Cyathocaulis and Cibotiocaulis, which, although generally resembling modern types, showed interesting differences in detail. For instance, the margins of the moristeles projected inwards and root-traces occurred in the medulla. Another fossil tree fern (Dendropteris cyatheoides) from the volcanic series of Mount Elgon, East Africa, was described by Bancroft (1932). In 1932 also, Godwin described the complex vascular arrangements in the stem of Cyathea medullaris.

It is clear from the above survey of the literature that most of the anatomical investigations on the Cyatheaceae and related forms have been concerned with the general features of the variable and complex vascular system of the stems. Less attention has been paid to other features, such as the detailed histology of the various tissues, the structure and development of the stomata, the anatomy of the fronds, and the structure and development of the dermal appendages. As Holttum has indicated, more facts about such features are needed as a contribution to the solution of the difficult taxonomic problems presented by these ferns.

Cyathea Smith (1793)

Introduction

The majority of the species of Cyathea are tree ferns with erect stems, the younger part of which is protected by broad, chaffy scales. The huge fronds are usually rhomboidal, mostly bipinnate or more highly dissected, or, very rarely (e.g. in C. sinuata) simple, and are spirally arranged in a crown. During the early stages of development they are protected by scales and hairs, the latter being simple or branched. In some species (e.g. C. capensis), near the base of the petiole, there are modified frond-like structures, known as aphlebiae.

The veins are free apart from very rare fusions, and the sori, which are superficial at maturity, are borne on them or in their axils. The sporangia are borne in gradate sequence on the hemispherical to globose receptacles, and may have an inferior, cup-like or flap-like indusium, or the indusium may be absent. Paraphyses are commonly associated with the sporangia, which usually have stout stalks. The oblique annulus has a definite stomium and lateral dehiscence. The spores are tetrahedral.

Previously it was the custom to separate the species of this genus into three genera: Cyathea (with cup-like indusium), Hemitelia (with flap-like indusium), and Alsophila (without any indusium). Studies of Smith (1877), more recently of Copeland (1947), and Holttum (1954) show that this distinction is quite artificial, and the present practice is to place all the species in one large genus Cyathea, this being the earliest of the generic names.

The genus in its broad sense, includes about 700 species (Christensen, 1938).

Cyathea contaminans (Wall.) Copel

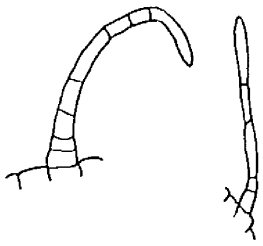

Fig. 1

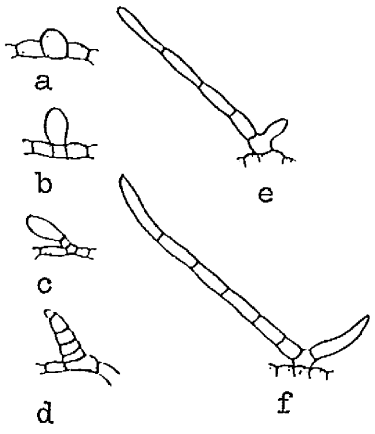

Fig. 3

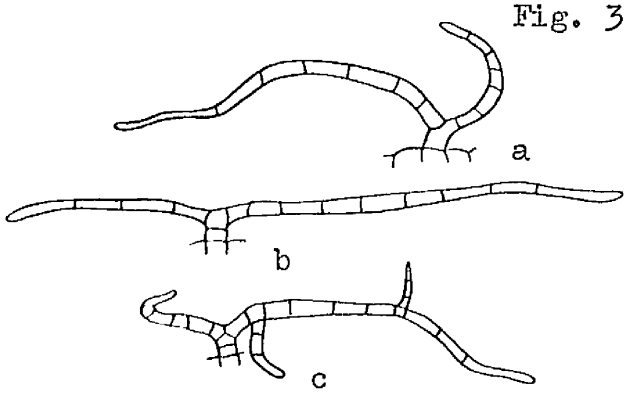

Fig. 2

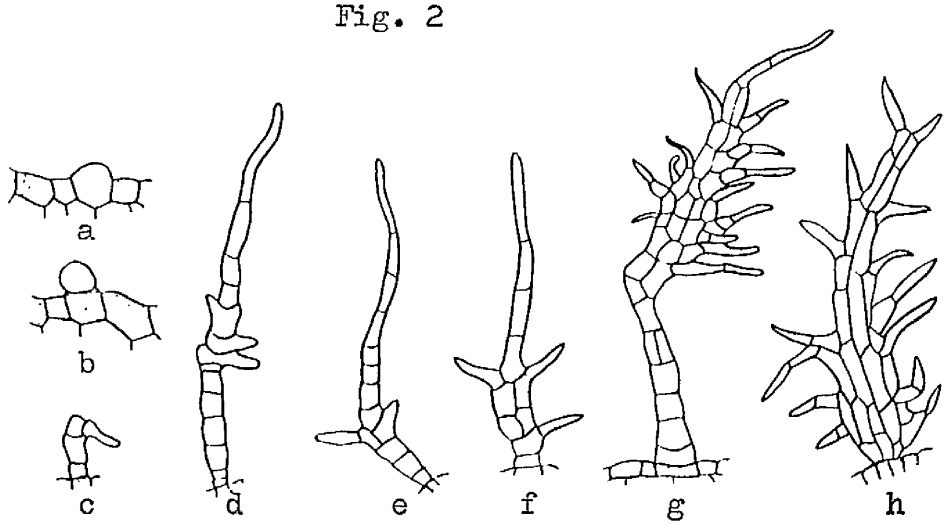

Fig. 4

Fig. 1, Unbranched hairs. Fig. 2. Hairs showing various types of branching. Fig. 3. Stages in the development of hairs. Fig. 4, Stages in the development of scales showing uniseriate condition during ontogeny.
(1, 2, 3, 4 c-h, x 50; 4 a and b, x 100.)

Cyathea contaminans (Wall.) Copel.
(= Alsophila contaminans Hook.)

Cyathea contaminans is one of the most outstanding types, being the largest among the tree ferns of the Malay Peninsula. At the same time it is anatomically one of the least investigated.

YOUNG PLANT

The material for this investigation was obtained from the Royal Botanic Gardens, Kew, and from Singapore, through the kindness of Professor R.E. Holttum.

HABIT

The stem of the young plant is erect, unbranched and cylindrical with an obconical base. The lower part of the stem is covered with the remains of petioles of old leaves and with numerous much branched adventitious roots, most of which are too short to reach the soil. At the distal end of the stem there is a crown of several leaves of varying ages, the younger ones showing circinate vernation. The stem apex and the young leaves are protected by hairs and scales in various stages of development.

ANATOMY

(a) Epidermis and Dermal Appendages

The epidermis is single layered and is composed of living cells whose outer walls are cutinised. It is, however, short lived and is peeled off as the stem ages. From the young epidermal layer develop the scales and hairs. The hairs are usually uniseriate. Some of them remain unbranched with either straight or curved tips (fig. 1); others branch in various ways (fig. 2). Developmental stages are shown in

Cyathea contaminans (Wall.) Copel.

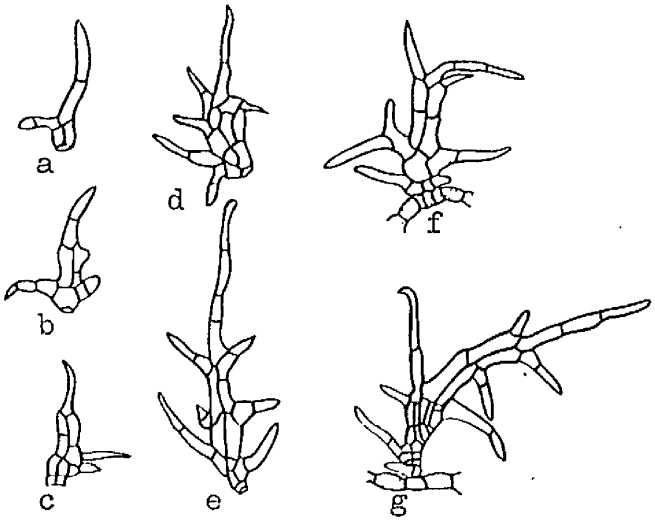

Fig. 6

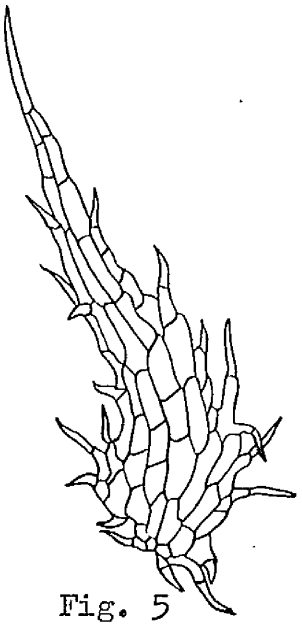

Fig. 5

Fig. 5, A setiferous scale. Fig. 6, Stages in the development of scales showing omission of uniseriate condition during ontogeny. (All, x 50.)

fig. 3 . An epidermal cell enlarges radially and divides to give an inner cell, which is the basal cell of the hair, and an outer cell, which, by further transverse divisions, forms the multicellular hair. The outer cell or, later, any of its daughter cells, may form a lateral projection (fig. 3,e) which, after being cut off from the parent cell by a wall, proceeds to divide transversely. In this way a branched hair is formed. Further branching of the hair may follow by the same process (fig. 2,c).

The flat scales (fig. 5), consisting of elongated cells, are pale when young, but at maturity become brown. Rigid, pointed setae, which become conspicuously brown with age, develop laterally from the edges of the scales. Such scales are referred to by Holttum as setiferous scales.

A scale develops from an initial cell which is easily distinguishable by its larger size and denser protoplast (fig. 4,a). The scale initial enlarges and divides by a transverse wall into two daughter cells - the outer and the inner (fig. 4,b). The inner cell contributes to the stalk of the scale and may remain undivided throughout (fig. 6,g) or may undergo longitudinal divisions, giving two, three, or more cells (fig. 4,h). If there is a longitudinal division in the basal cell, it always takes place after the upper cell and its derivatives have formed a few segments. The behaviour of the upper cell is quite variable. At first it may give rise to a series of cells due to successive transverse divisions of this cell and its derivatives (fig. 4,d), and then both transverse and longitudinal divisions take place irregularly, resulting in a scale several cells in length and width (figs. 4,e-h). Frequently the upper cell and its derivatives undergo irregular transverse and longitudinal divisions so that the uniseriate stage is omitted (fig. 6).

Cyathea contaminans (Wall.) Copel.

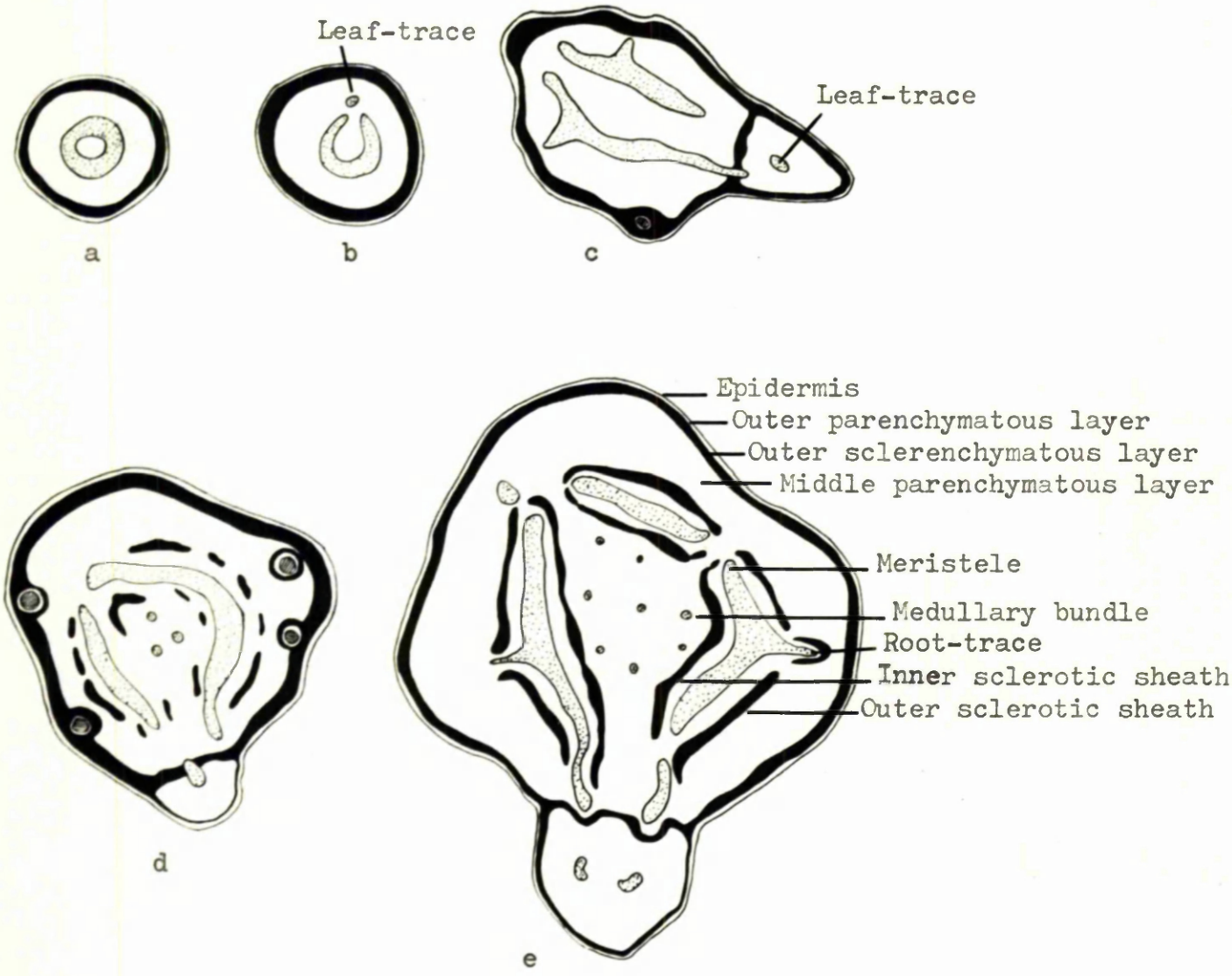

Fig. 7. Transverse sections of a stem at different levels. (All, x 5.)

Cyathea contaminans (Wall.) Copel.

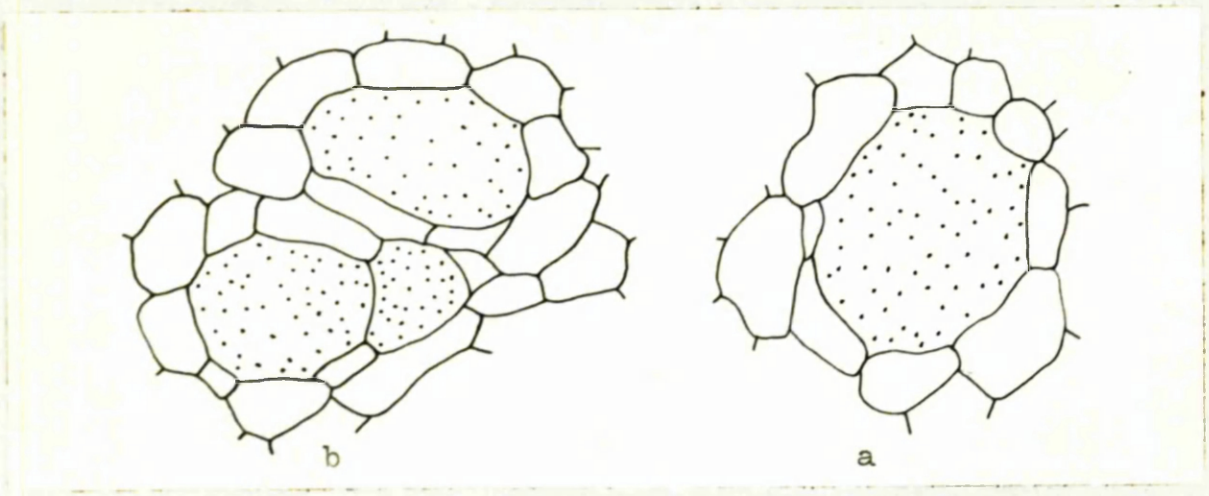

Fig. 8. Mucilage sacs. (Both, x 160.)

From the young stage onwards, some of the marginal cells of the scale proper form setiform projections which afe cut off from the mother cells by walls.

(b) The Cortex

The structure of the cortex is variable in the same plant in different regions. A transverse section very near to the base of the stem (fig.7a) shows that the cortex is made up of only three layers. The outermost is a layer of parenchymatous cells without intercellular spaces and with walls which are thicker than those of the ordinary parenchyma. There is a gradual transition between these cells and those of the next layer, which are stout spindle-shaped fibres. These two hypodermal layers constitute the protective tissue of the stem after the epidermis has peeled off. The third layer, which comprises the bulk of the cortex, is composed of parenchyma with intercellular spaces. These cells are packed with starch grains. In sections cut a few mm above the base, the cortex consists of the same type of tissue, but within the inner parenchymatous layer, there are present mucilage sacs, which may be isolated from one another or, more often, occur in groups of two, three or more (fig. 8). In longitudinal sections they are found in irregular vertical rows. Often two or more sacs unite at their ends and form a continuous tube that ends blindly. The mucilage turns violet with H_2SO_4 and Iodine. It also stains a deep blue with methylene blue. A transverse section at a higher level (fig.7,d) shows the appearance of patches of sclerenchyma within the inner cortex. These form a discontinuous ring lying almost parallel to the vascular tissue.

In a transverse section at a still higher level, it is seen that the inner parenchymatous layer has become differentiated into three distinct layers (fig.7,e). Two parenchymatous layers

are separated by a stout zone of sclerenchymatous cells. So in this region the cortex consists of five distinct layers, which are as follows: i. the outer layer of parenchymatous cells, ii. the sclerenchymatous sheath of the stem, iii. the middle parenchymatous layer, iv. the hard sclerenchymatous outer sheath of the vascular tissue, and v. the inner zone of parenchymatous cells with intercellular spaces. In this last zone there are no mucilage sacs at this level, but higher up there appear numerous mucilage sacs similar to those in the middle parenchymatous zone. The sclerenchyma is separated from the parenchyma on each side of it by a layer of short, almost isodiametric cells. These cells are living, devoid of starch grains and are peculiar in having the wall adjacent to the sclerenchyma very strongly thickened while the opposite wall remains thin (see fig. 27). Each of them contains a crystalline substance. Ogura (1927), in his description of Japanese Cyathea spp. refers to these cells as cubical cells, but does not mention anything about their crystalline inclusions. Cortical vascular bundles, which have been found in some spp. of Cyathea, are absent in Cyathea contaminans.

(c) The stele

The extreme base of the young plants available for examination had already decayed so that it is not possible to give a complete account of the stelar ontogeny. The series of transverse sections which will now be described will, however, serve to indicate all but the earliest stages in the development of the characteristic Cyathean stele.

The lowest sections already show a solenostelic condition (fig. 7,a). The first leaf-trace departing from this solenostele consists of three strands, one of which passes to the abaxial and two to the adaxial side of the leaf base. The former

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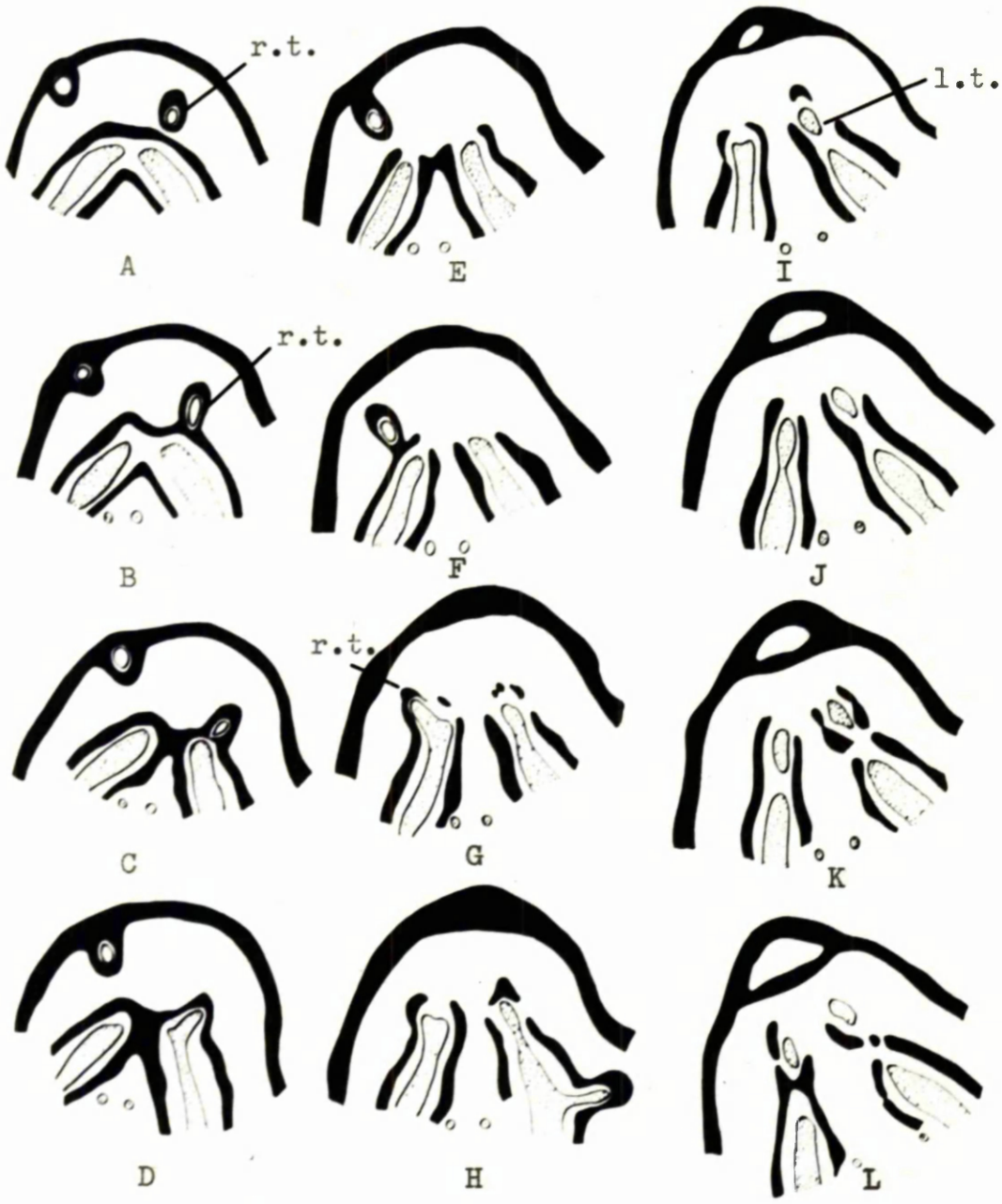

Fig. 9. Selected sections (arranged in acropetal order) from a transverse series, showing departure root-traces (r.t and leaf-traces (l.t.) from a node at higher level.
- Explanation in the text. (x 6.)

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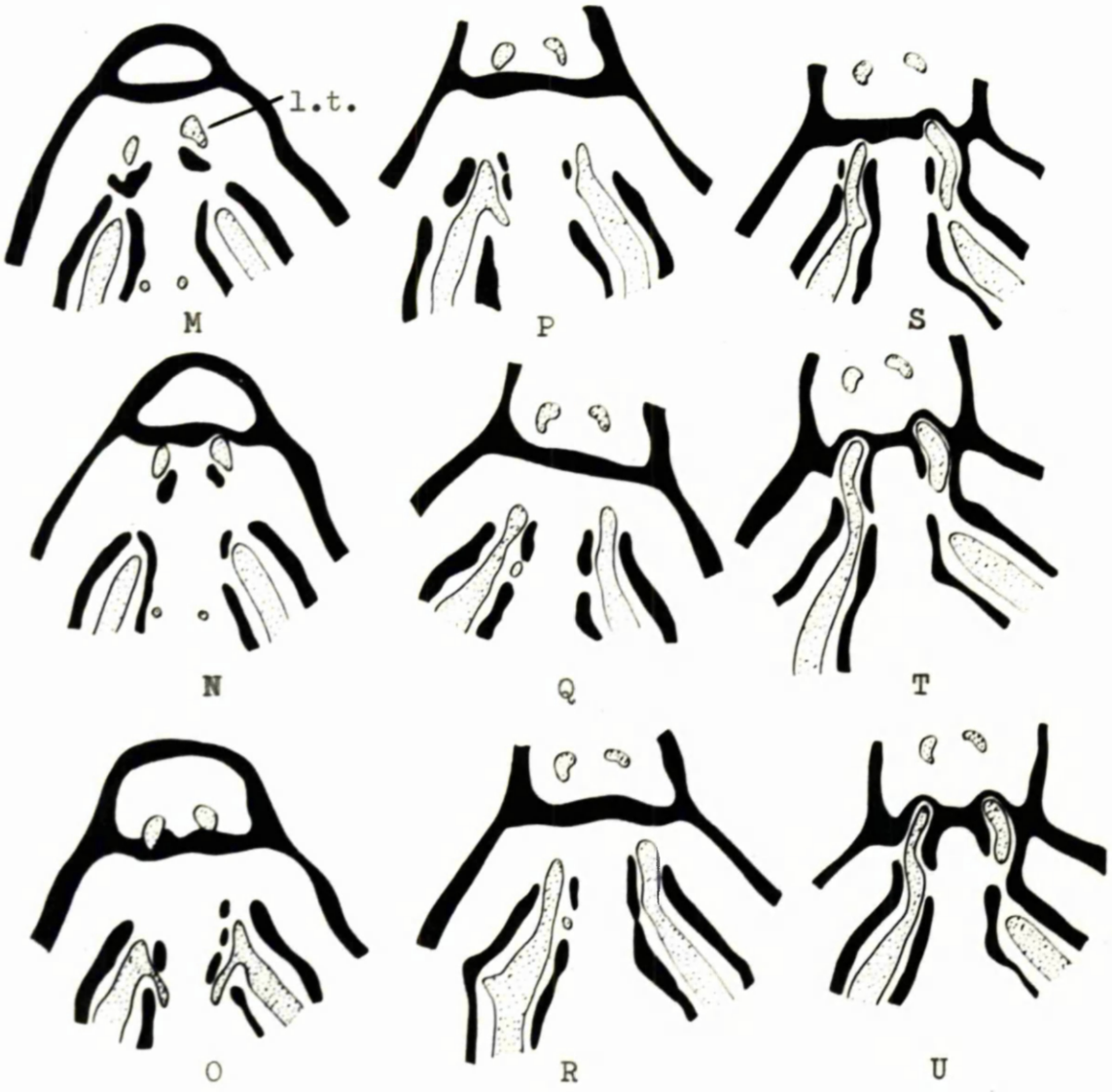

Fig. 9. Contd.

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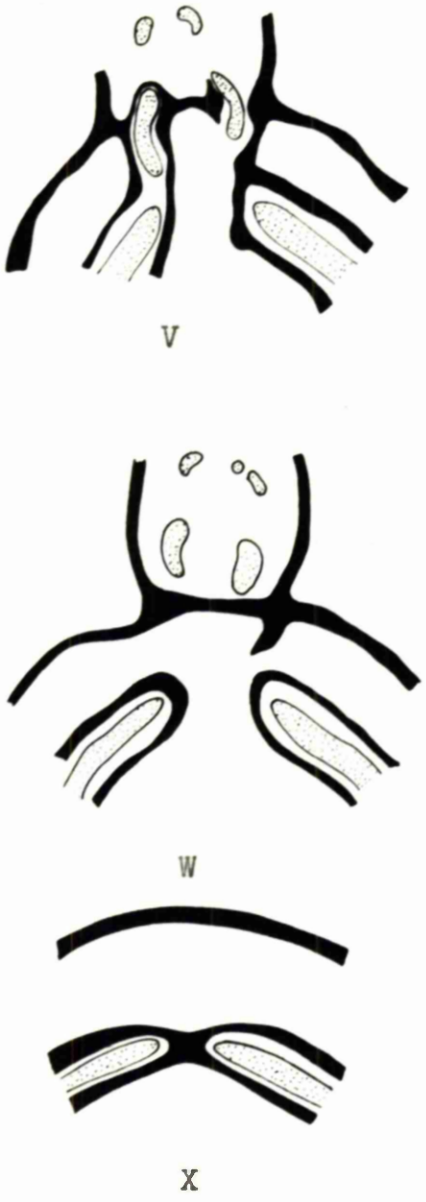

Fig. 9. Contd.

departs from near the base of the associated leaf-gap while the latter depart, one from each side of the gap, at a slightly higher level (fig. 7, b). This gap closes at about the same level as the next higher gap is opening. The latter, however, definitely overlaps the gap associated with the next higher leaf and in this way a dictyostelic condition is established (fig. 7, c). The successive leaf gaps in this region only slightly overlap one another, so that while some sections show two gaps, others show only a single one. Near the apex of the young plant the fronds are more closely inserted and their leaf gaps overlap to a greater extent so that the higher sections of the series all show either two or three leaf gaps (fig. 7, e).

The departure of the leaf-traces at one of these higher nodes is illustrated in fig. 9 by selected sections from a transverse series arranged in acropetal order. Fig. 9 , A-G, shows the opening of the gap in the vascular tissue and, at a slightly higher level, the opening of gaps in the sclerenchymatous sheaths. These figures also show the insertion of root traces, one from each edge of the gap, and the downward and outward passage of these. Fig. 9 , H-P, shows the departure of the two abaxial strands of the leaf-trace from the sides of the leaf-gap and their passage outwards into the petiolar base, traversing in their path the sclerenchymatous plate between the latter and the stem. The departure of the adaxial traces follows at a slightly higher level and the path of these into the petiole base is indicated in fig. 9 , Q-W. Above this level the leaf gap narrows, the sheaths of the two meristeles unite again, and ultimately the leaf-gap is completely closed.

In addition to the main stelar system described above, the stem of Cyathea possesses an accessory system of medullary bundles, the origin and structure of which will now be described. This accessory system first appears at a level

where the dictyostelic condition has been established. Fig. 10 illustrates the origin of a medullary bundle as a projection of vascular tissue from the inner surface of a meristele. This projection then becomes free as a medullary bundle which, at a slightly higher level, fuses again with the meristele at the margin of the leaf-gap. At higher levels (e.g. fig.7,d and e) an increasing number of medullary bundles form an anastomosing system. Some of these strands arose, like the first one, from the inner surface of a meristele. Others arose de novo from cells of the medulla and thus end blindly below. Strands of this medullary system unite at higher nodes with leaf-gap margins, often at a level near the departure of the adaxial leaf-traces. An example of this behaviour is shown in fig. 9 , M-O, where two medullary bundles, which at lower levels were running vertically in the pith, turn sharply outwards and, passing through the inner sclerotic sheath, unite with the meristeles, one to each side of the gap. Sometimes, as in this example, one of the bundles becomes free again before again uniting with the same meristele (fig. 9 , P-S).

(d) Anatomy of meristeles and medullary bundles

The meristeles are surrounded by an endodermis which consists of cells which are elongated tangentially and show casparian strips on their radial walls. The endodermal cells can often be recognised just below the apical region of the stem by their tanniniferous contents, apart from the characteristic thickening on their radial walls. Below this level they do not show such high tannin content.

The pericycle zone comprises 1-3 layers of parenchymatous cells. The cells have thin walls and do not contain any starch grains. Each meristele is a hadrocentric (amphicribral) bundle with xylem surrounded by the phloem. The xylem is

mesarch and contains a lot of parenchyma amongst the tracheids. Vessels are absent. Except for occasional tracheids with helical thickening in the very ill-defined protoxylem, the entire xylem mass is composed of tracheids with scalariform pitting. These tracheids measure about 300 to 850 u in length and 32.5 to 63 u in breadth. The wall of a scalariform tracheid measures about 5.5 u in thickness.

The xylem parenchyma consists of more or less elongated cells placed in vertical series. Their walls are thick and slightly lignified. Tannin occurs in the protoplast of these cells and impregnates their walls. It often forms small rounded bodies which sometimes fuse into masses in the cytoplasm and completely mask the nucleus. Whatever may be the physiological functions of these tannin filled xylem parenchyma elements, they certainly increase the mechanical support of the plant. The cells of the xylem parenchyma have an average length of 250 u and breadth of 42.5 u.

The phloem is composed of sieve cells and phloem parenchyma. The sieve cells are arranged end to end. They are relatively narrow in the young stem and have sieve areas on all walls. Often the sieve areas are in linear rows. A mature sieve cell which is enucleate, has an average length of 185 u and breadth of 25 u. The protophloem, which is bounded externally by the pericycle, consists of a very ill-defined layer of sieve cells. Immediately within the protophloem layer there lies a layer of cells, usually 2-3 cells deep. These cells are elongated tangentially in a transverse section; hence they are cut transversely in a radial longitudinal section of the stem. Zenetti (1895) found a similar type of cell in Osmunda and termed them "quergestreckte zellen". Ogura (1927) also recorded the presence of such cells in his description of Cyathea ogurae

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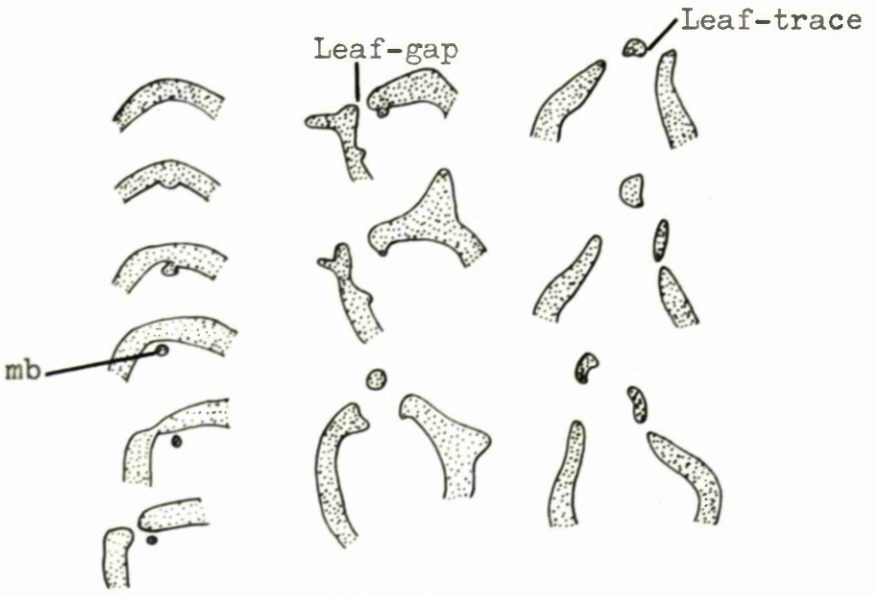

Fig. 10

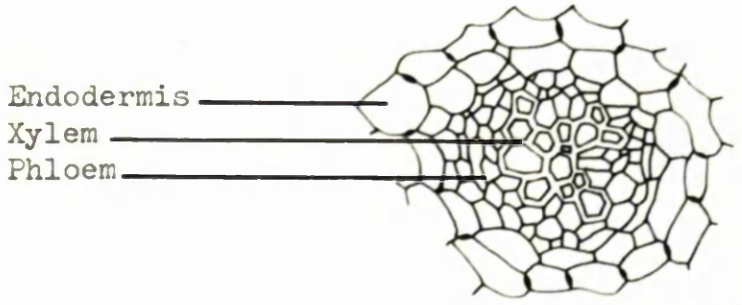

Fig. 11

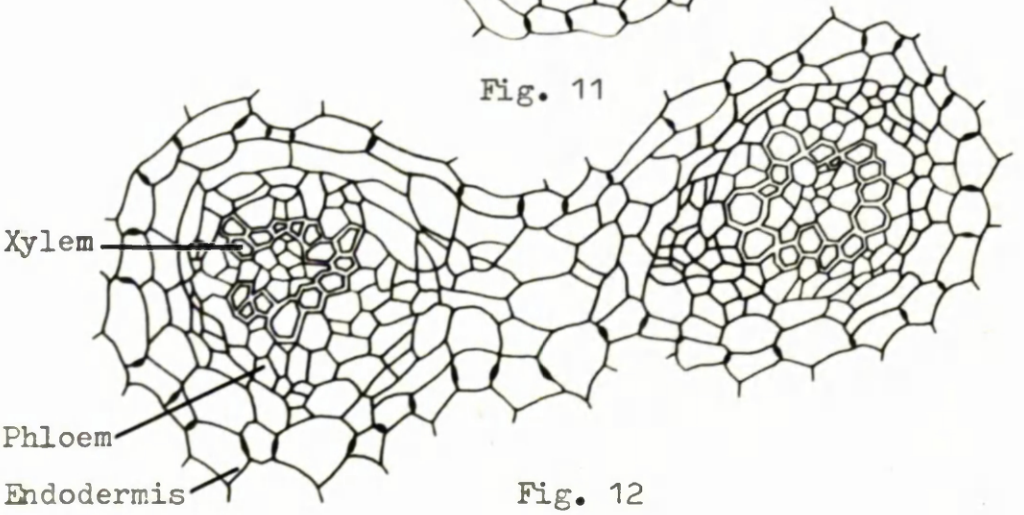

Fig. 12

Fig. 10. Diagram showing the origin of a medullary bundle (mb) as a projection of vascular tissue from the inner surface of a meristele. Fig. 11. A medullary bundle. Fig. 12. A medullary bundle showing bifurcation. (10, x 6; 11, 12, x 220.)

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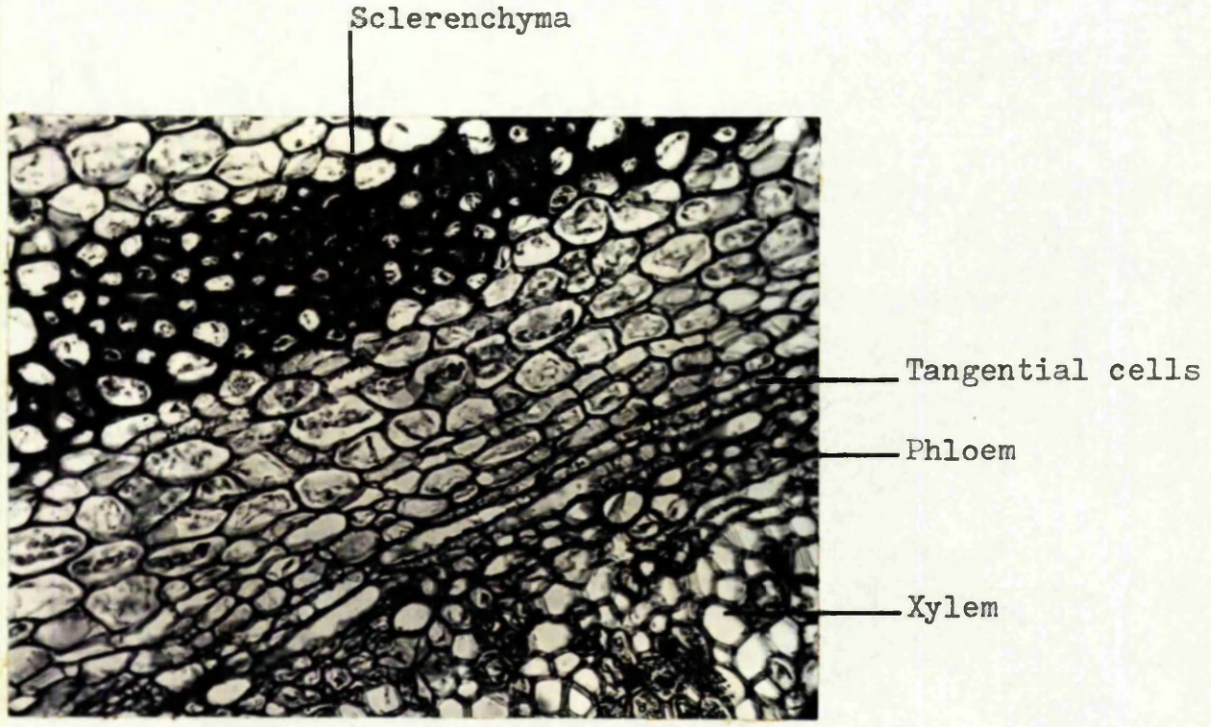

Fig. 13. Part of a transverse section of a stem. (x 83.)

(Alsophila ogurae Hayata) under the name "tangentially elongated cells", or briefly "tangential cells". These cells are devoid of nuclei, and have sieve areas on all walls (fig.13). In fact, apart from their orientation and slightly thicker walls, they are exactly like the normally oriented sieve cells of the metaphloem. Another distinction is that the tangential cells in this species are sometimes filled with mucilaginous substances. Inside the layer of these peculiar cells, lies the metaphloem. The phloem is separated from the xylem by parenchyma, although sometimes a sieve cell lies directly against a scalariform tracheid.

The medullary bundles are more or less circular in transverse section and each is surrounded by its own endodermis with characteristic thickening (figs.11,12). The pericycle consists of a single layer of parenchymatous cells. The bundles are amphicribral, with or without parenchymatous tissue in the centre. The protoxylem, which is endarch, is composed of tracheids with helical thickening. The metaxylem consists of scalariform tracheids and xylem parenchyma. The xylem parenchyma, unlike that in the meristeles, does not show any lignification of the walls or tanniniferous contents in the cytoplasm. The phloem of the bundles is composed of sieve cells and phloem parenchyma which are structurally similar to those of the meristeles. The "tangential cells" which lie adjacent to the phloem in the meristeles are not present in the medullary bundles.

(e) The Medulla

The medulla, with its system of bundles described above, increases in anatomical complexity from the base of the young plant upwards. At the base of the plant the medulla consists of rather loosely arranged parenchymatous cells with intercellular spaces. At this level, mucilage sacs are absent.

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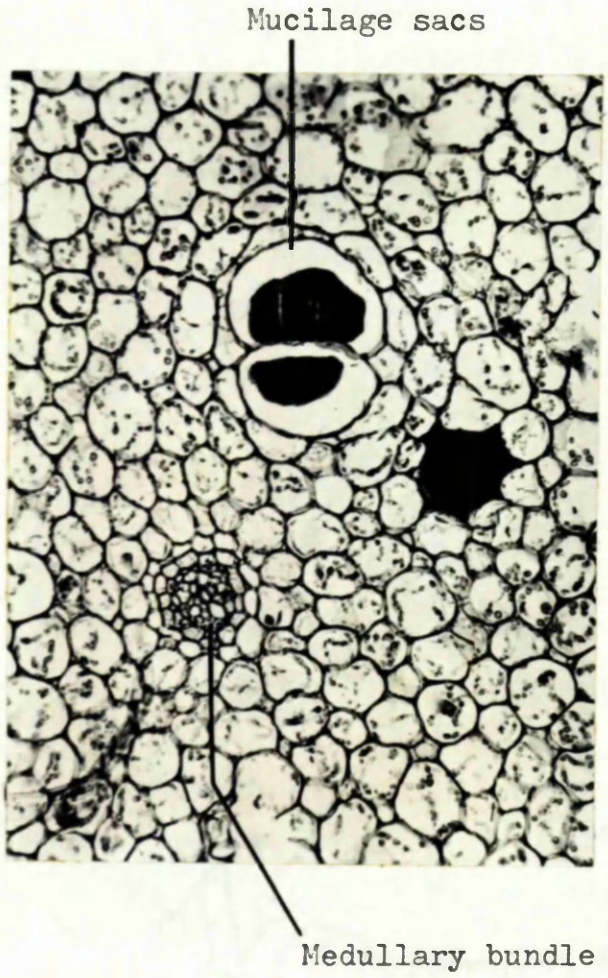

Fig. 14. Part of a transverse section of a stem. (x 90.)

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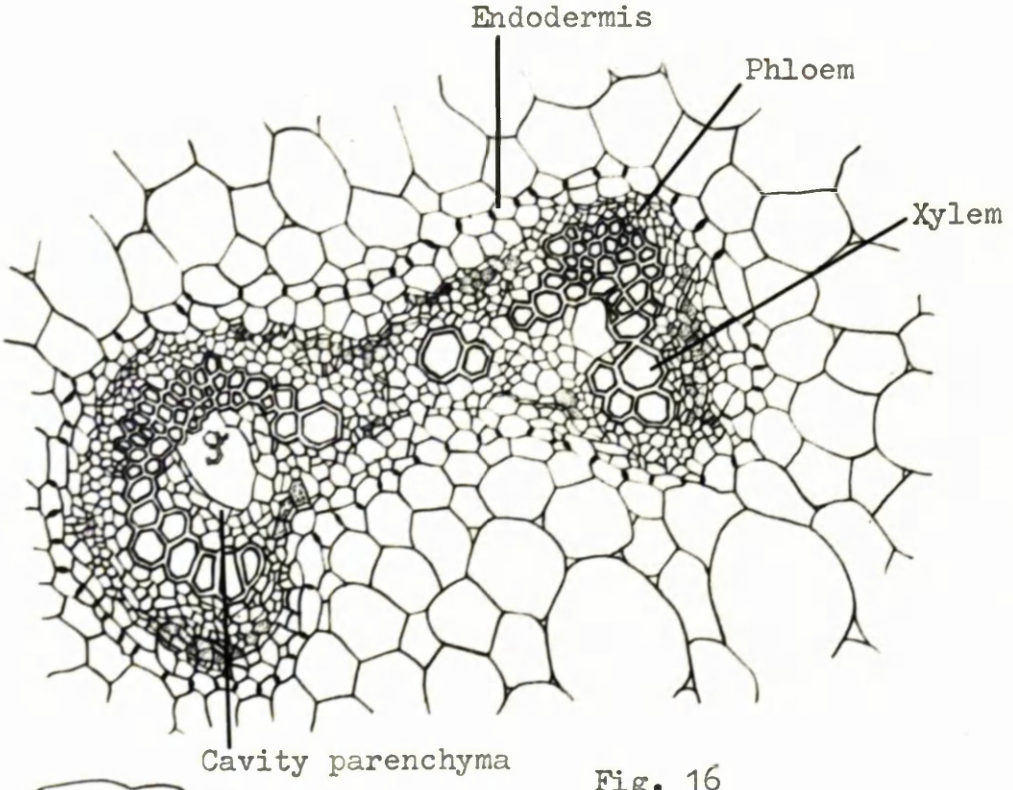

Fig. 16

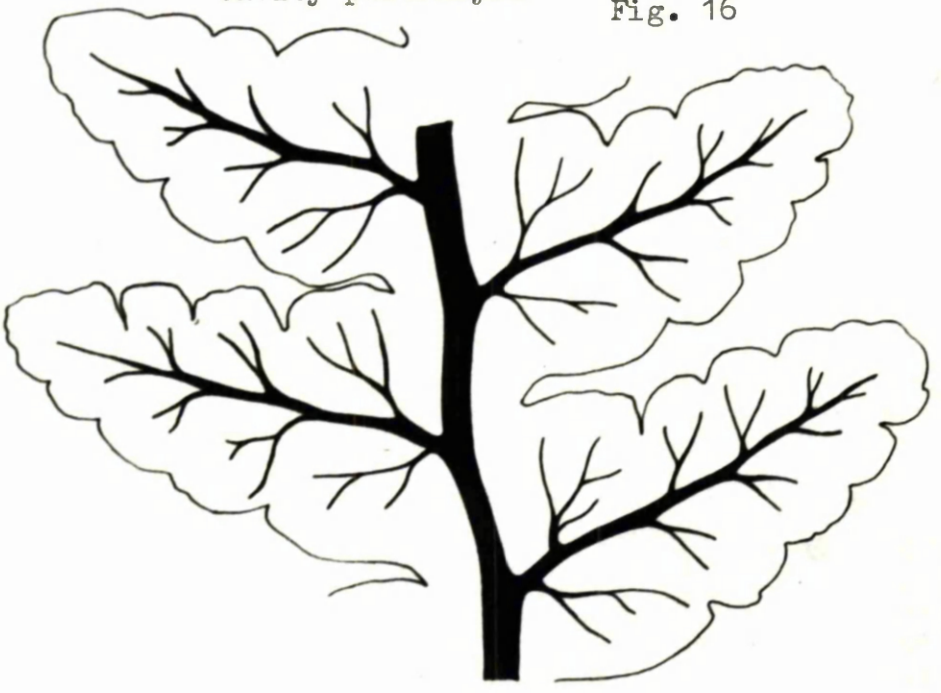

Fig. 15

Fig. 15. Part of a frond showing open venation.
Fig. 16. Transverse section of a petiolar bundle.
(15, x 9; 16, x 160.)

A few mm above the base a strand of sclerenchyma appears in a central position, but, as serial sections show, this soon dies out and the pith becomes entirely parenchymatous again. At still higher levels the pith is differentiated into three distinct layers (fig. 7, e). Two parenchymatous zones are separated by a layer of sclerenchymatous cells, the latter being the inner sheath of the stele. Mucilage cells, similar to those in the cortex (fig. 14) are present in the central mass of parenchyma.

THE FRONDS

(a) External Form. The fronds are tripinnate. After the death of the fronds the bases of the stipes persist and form one of the components of the protecting sheath of the stem. A mature frond of an old plant of this species is known to be among the largest produced by tree ferns. A frond of a young plant investigated, however, measured 70 cm in length. In such a frond, the stipe occupies about one fifth of its entire length. Both the stipe and rachis are purplish in colour, but in the young stage they are glaucous and are covered with scales and hairs, most of which fall off at maturity. After the scales are shed, the cells of the persistent bases divide actively and form thorn-like projections, composed of elongated fibres. However, the stipe and rachis of a young plant are not so strongly thorny as those of an old plant. The pinnules are sessile with a truncate base and acuminate apices; the margins are lobed. Veins divide dichotomously and are open (fig. 15). The texture of the frond is leathery.

(b) Internal structure of the stipe and rachis. The persistent bases of the series of fronds produced by a young plant during its development show an increasing complexity of their vascular supply. The lowest stipe observed has a single vascular strand in which the vascular elements are segregated

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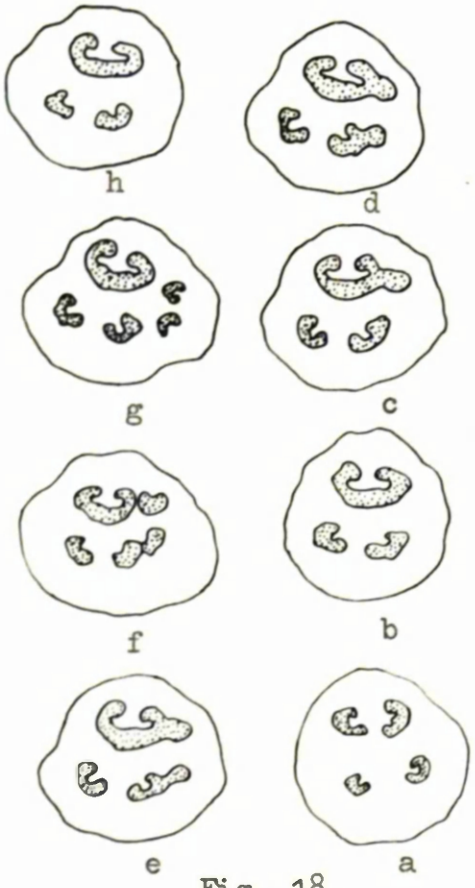

Fig. 18

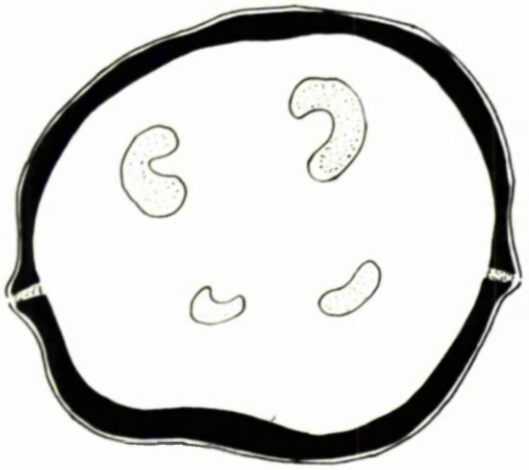

Fig. 17

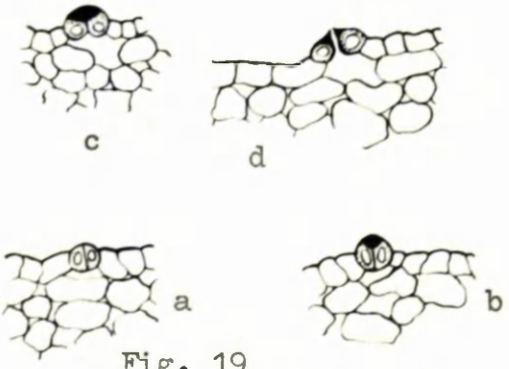

Fig. 19

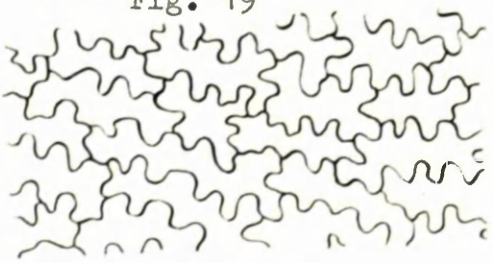

Fig. 20

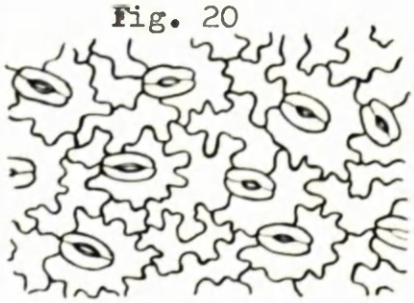

Fig. 21,a

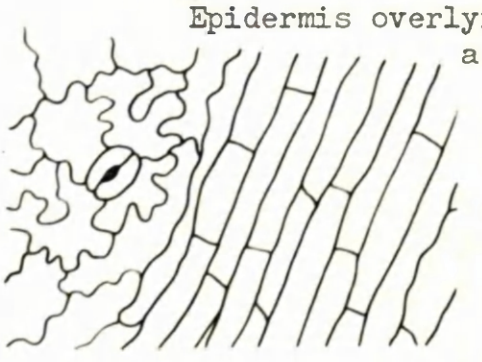

Fig. 21,b

Fig. 17. T.S. of a petiole.
Fig. 18. Serial transverse sections through the frond axis, showing the fusion between the members of the adaxial strands and also among the members of the abaxial series. Extra-marginal origin of the pinna-traces is also shown.
Fig. 19. Stomata in sections. Fig. 20. Epidermis on the adaxial surface of the lamina. Fig. 21. Stomata on the abaxial surface.
(17, x 22; 18, x 18; 19, x 205; 20 and 21, x 130.)

into three groups. The stipes of higher leaves show three separate strands, one abaxial and two adaxial (fig. 30), while those of the functional leaves at the top of the young plant have four or five strands (fig. 17). An example of this last type will be described in detail.

In transverse section the base of the stipe is more or less circular or oval, sometimes with two lateral ridges (fig. 17). The epidermis is one cell thick and consists of living cells. Its outer wall is rather thick and cutinised. In longitudinal section the epidermal cells are much elongated and rectangular in outline. The cells of this layer give rise to scales and hairs similar to those borne on the stem. The epidermis is interrupted at intervals by pneumathodes. The hypodermis is a sheath of sclerenchymatous fibres several cells thick. The remaining ground tissue is parenchymatous and mucilage sacs, similar to those found in the stem, are present. Out of the four or five petiolar traces, two are adaxial in position, the remaining ones are abaxial. This arrangement is continued into the rachis, but towards the tip the two adaxial strands fuse and, at a still higher level, fusion of the abaxial strands also occurs, so that here there is a single abaxial and a single adaxial strand (fig. 18,d). The extra-marginal origin of the pinna traces is also shown in fig. 18 .

(c) Structure of petiolar bundles. Petiolar bundles may be L, V, or W-shaped structures (fig. 17), the last type corresponding to two fused L or V-shaped bundles. The endodermal cells of a petiolar bundle (fig. 16), apart from their characteristic thickening in the radial walls, may contain tanniniferous substances, colouring the cytoplasm The pericycle consists of one or two layers of thin-walled cells. The sieve cells of the protophloem form an almost continuous layer inside the pericycle. In longitudinal

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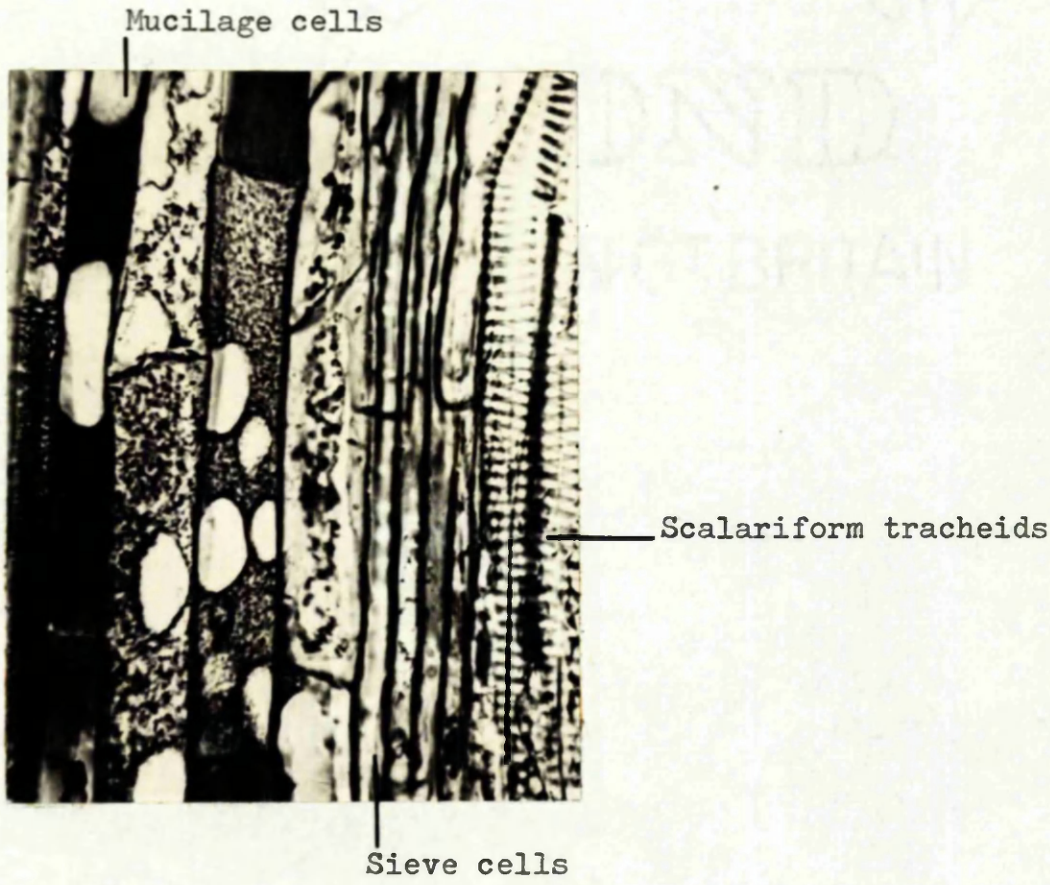

Fig. 22. Mucilage cells associated with the sieve cells of the petiole (longitudinal section). (x 270.)

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Fig. 23. Longitudinal section of the petiole showing penetration of parenchymatous cells into the lumen of the tracheids. (x 270.)

sections the sieve cells of the metaphloem are very prominent and form continuous vertical series. The sieve cells are slender and elongated and have sieve areas on all walls; their end walls are usually slightly oblique; they measure about 360 u in length and about 10 u in breadth. Associated with the sieve cells, are found several thin-walled cells containing mucilage. A longitudinal section shows that those cells are arranged in vertical series, and that the individual cells are characterised by the presence of large vacuoles (fig. 22). These cells have an average length of about 150 u, and breadth of about 18 u. The xylem is usually separated from the phloem by the conjunctive parenchyma. The metaxylem is composed of scalariform-pitted tracheids and a few xylem parenchyma elements. The latter, like those of the stem xylem, may show the presence of tanniniferous bodies, but their walls do not give any lignin reaction. The length of the metaxylem tracheids varies from 300 to 415 u, and their diameter from 20 to 35 u. The protoxylem is made up of tracheids having annular to helical thickening. At maturity the protoxylem becomes crushed and lies adjacent to 'cavity parenchyma' (fig. 16).

The cavity parenchyma, which lies adjacent to the protoxylem of the petiole, consists of loosely arranged, comparatively large parenchymatous cells (fig. 16). Fig. 23 shows the penetration of certain parenchymatous cells into the lumen of a tracheid with annular-helical thickening. These parenchymatous cells are actually the outgrowths of some of the conjunctive parenchyma, which separated the xylem from the phloem. The penetration of these outgrowths into the annular-helical tracheids takes place soon after the differentiation of the protoxylem elements, and is best seen in a longitudinal section of a circinately coiled frond or of a tip of a comparatively young frond. Immediately after the penetration,

the intruding parenchymatous cells begin to enlarge and ultimately break the walls of the invaded tracheid, resulting in a protoxylem cavity, filled with these loosely arranged cells. The walls of these parenchymatous cells often attain considerable thickness. In a transverse section of the base of a very mature petiole, it is seen that these loosely arranged cells, which at one time broke the walls of the protoxylem, have disintegrated, leaving a cavity, sometimes with fragments of protoxylem elements within, even when the adjacent thin-walled cells are found to be functional and quite active (fig. 16). These cavity parenchyma cells thus differ from tyloses, which do not disrupt the xylem elements in which they have developed, but remain as balloon-like intrusions. Various theories have been postulated as to the functions of the cavity parenchyma in the ferns. It seems that the cavity left after the disintegration of the protoxylem and invaded parenchyma cells, acts as a store house of water in the petiole.

(d) Pneumathodes. Pneumathodes occur in discontinuous rows along the two sides of the petiole and rachis. They are not readily seen on young fronds but become increasingly conspicuous as the fronds mature. In the region of a young pneumathode the hypodermal band of sclerenchyma is replaced by aerenchyma which is covered by the epidermis with stomata. The stomata are short lived. As the frond matures the epidermis and the aerenchyma of the pneumathode become necrotic and as a result of this a cavity filled with loosely aggregated dead cells with suberised walls is formed. This powdery tissue is in contact with the living parenchyma of the ground tissue and thus provides a ventilating channel through the sclerotic hypodermis.

(e) The lamina. The cutinised epidermal cells on both surfaces of the lamina have wavy anticlinal walls (figs. 20, 21) but over the veins they are elongated and have straight walls. Stomata are present only on the abaxial surface, and they occur both over the veins and the intervening mesophyll. The mesophyll is not differentiated, but the cells are more compact on the upper surface than on the lower, where more conspicuous intercellular spaces are found. The traces are collateral in structure. Although lacking the characteristic thickening, the endodermal cells of the veins are recognisable by their tannin content. The traces have protoxylem facing the adaxial side and phloem the abaxial one. The phloem, however, is not very well developed. Xylem parenchyma and mucilage cells are, however, very conspicuous.

(f) The stomata. The oval stomata usually have a subsidiary cell. They measure about 45 by 25 u. The walls of the guard cells are unevenly thickened and there are ledges of cutinised wall material, appearing as horns in sections, projecting over the external opening of the stomatal pore (fig. 19,d). The differentiation of the stomata was followed in sections of laminae of varying ages. The stoma mother cells are readily distinguishable since they have denser protoplasts and larger nuclei than the surrounding cells of the protoderm. The mother cell then divides by an anticlinal wall to give the two guard cells (fig. 19,a). The walls of these now become differentially thickened and cutinised, the outer walls being the most strongly thickened (fig. 19,c). Following the dissolution of the intercellular material between them the two guard cells separate to form the stomatal pore (fig. 19,d). There does not appear to be any definite sequence in the development of the stomata on a young leaf and frequently various developmental stages can be observed near to

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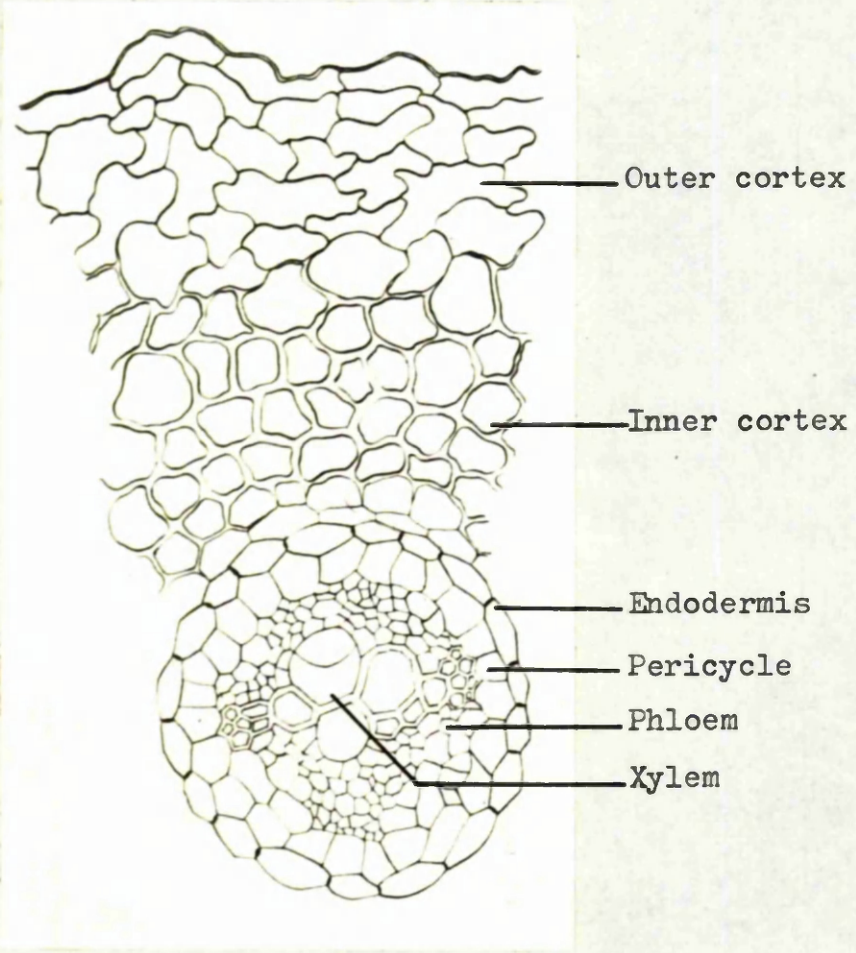


Fig. 24. Transverse section of root. (x 275.)

mature stomata.

THE ROOT SYSTEM

The obconical stem of the young plant is clothed with numerous, richly branched, roots which developed in acropetal sequence as the plant grew. The uppermost roots developed just below the crown of functional leaves and these, with others arising just below this level, had not yet reached the soil.

The root anatomy is similar to that of other advanced ferns (fig. 24). The piliferous layer bears a zone of root-hairs just behind the apex but in the basal region no root-hairs are present. The structure of the cortex varies at different levels. In the root-hair region it is entirely parenchymatous but above this level the inner cortical cells become strongly lignified, while the outer zone of cells remain thin-walled (fig. 24). In the basal region of the root the entire cortex is strongly lignified.

The diarch stele is surrounded by a primary endodermis and a one to two layered pericycle. The spiral tracheids of the protoxylem abut directly on the pericycle; the metaxylem consists of scalariform tracheids. In some otherwise mature roots the metaxylem tracheids remain thin-walled and unlignified, as in the root figured. The phloem is in two groups on the two sides of the bar of xylem.

The development and functioning of the Cyathean root system, which invests the stem of young plants and the lower regions of the stem of adult plants, are not entirely clear. It has been stated that many of the roots do not reach the soil and serve for the absorption of atmospheric moisture. Roots which do reach the soil serve both for absorption and as strut-roots supporting the obconical stem.

Cyathea contaminans (Wall.) Copel.

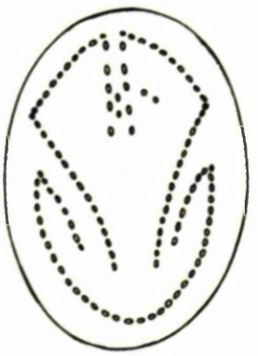


Fig. 25

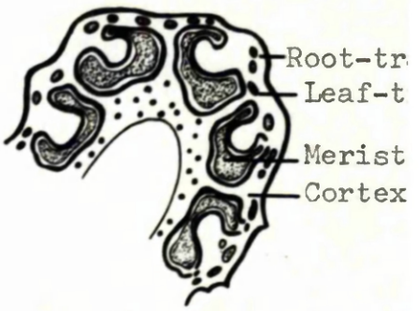


Fig. 26

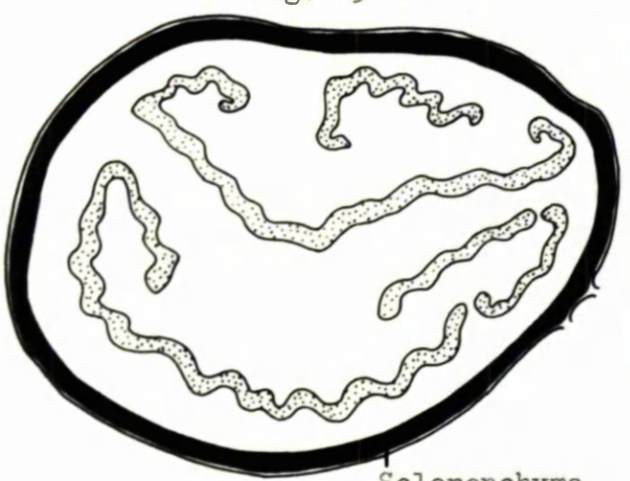


Fig. 29

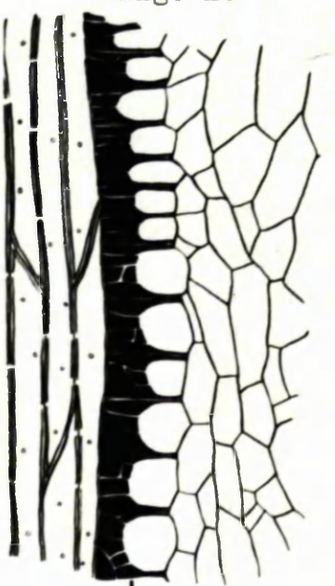


Fig. 27

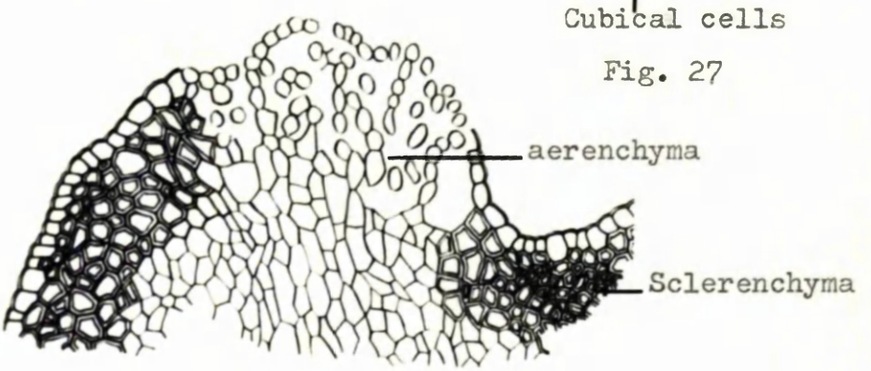


Fig. 28

Fig. 25. A leaf-scar showing the arrangement of leaf-traces. Fig. 26. T.S. of the stem. Fig. 27. L.S. through a part of the cortex showing the transition between parenchyma and sclerenchyma. Fig. 28. T.S. through a pneumathode. (25, x 3/5; 26, x 3/5; 27, x 156; 28, x 160; 29, x 5.)

ADULT PLANT

Pieces of dried stems together with herbarium sheets of the fronds of adult plants were made available to the writer through the courtesy of Professor H.J. Lam from Rijksherbarium. This material was collected in March 1939, during the third New Guinea Expedition of the American Museum of Natural History, at a distance of about 4 Km south-west of Bornhard camp, Idelburgh River, at an altitude of 850 m, where this plant was found growing very abundantly and was a conspicuous feature of low seral rain forest on the sandy banks of the river.

THE STEM

(a) External features. The single short length of stem examined came from a plant about 9.6 m in height and 12 cm in diameter under the leaves and with a diameter of over a meter through the base of a conical mass of adventitious roots covering the stem to the height of 2 m. This piece of stem showed several leaf-scars arranged in a very close spiral. These pale, oval leaf-scars measuring about 7.4 x 5.2 cm, are protected by hard sclerotic plates through which the remnants of the leaf-traces project. These traces, varying from 110 - 115 in number, are arranged in a definite manner, forming 3 groups, one of which is abaxial, while the other two are adaxial in position (fig. 25). The abaxial group resembles an arc, which is almost parallel to the lower margin of the leaf-scar. The ends of this arc bend inward and project downwards for a short distance. The adaxial traces are arranged in such a way that they form two groups, one resembling an inverted L ( ) and the other the numerical figure seven (7), facing each other. In addition to the bundles forming these three groups, there are four other isolated and irregularly arranged traces in the adaxial region.

Thomae (1886), and Ogura (1927) in their description of certain spp. of Cyathea, classified the petiolar bundles into abaxial and adaxial series, while Godwin (1932), in his description of Cyathea medullaris Sw. proposed a different and detailed nomenclature for them. But none of them found the four irregularly arranged traces in the species they described. As Bower has pointed out (Filicales vol. I, p. 168), this apparently complex arrangement was probably derived from the more primitive horse-shoe type leaf-trace in relation to increasing size of the leaf. The two deep lateral involutions between the abaxial and the adaxial series are clearly related to the presence of pneumathodes on the sides of the petiole.

Between the leaf-scars, all over the stem, there are remnants of compactly arranged brown setiferous scales, which resemble the scales of the young plants in all respects excepting their size. The thorns which are so abundant on the rachis and the petiole do not occur on the stem. Below the scales, the stem is covered with an extremely hard protective tissue.

(b) Anatomy. In a transverse section, the outline of the stem appears more or less irregular (fig. 26). The peripheral protective tissue, which measures about 1.5 mm in thickness, is composed of two almost equally thickened layers, the outer of which is much paler than the inner deep brown one. Within the protective layer lies the whitish fundamental tissue, with a varying thickness of .3 - 1.5 cm. At the periphery of the fundamental tissue, and in relation to leaf-gaps cut across at various levels, numerous leaf-traces with a diameter of 1 - 4 mm are found. These leaf-traces are surrounded by sclerenchymatous sheaths. The meristeles, about seven in number, are arranged in a ring, 5 - 5.5 cm in diameter. Each meristele is a U-shaped structure and is surrounded by a sclerenchymatous sheath

about 1 mm in thickness. The medulla, which varies from 2.5 - 5 cm in diameter, contains numerous bundles, which appear as brown dots to the naked eye.

Since the piece of stem available for examination is a Rijksherbarium specimen it was not possible to dissect it so as to investigate the mode of departure of the leaf-traces and the course followed by the medullary strands.

The detailed structure of the various tissues is similar in most respects to that already described for the upper part of the stem of a young plant. The cortical parenchyma contains mucilage sacs and a very characteristic feature, already noted in the young plant, is the occurrence of a layer of "cubical cells" at the junction between the sclerenchymatous sheaths and the surrounding parenchyma. In this layer the tangential walls adjacent to the sclerenchyma are very strongly thickened and are traversed by numerous pits; the radial walls are thickened to a lesser extent while the tangential walls adjacent to the parenchyma remain thin (fig. 27). These "cubical cells", although differing somewhat in shape from the corresponding cells in young plants, possess the same crystalline inclusions as the latter. Another feature occurring in both the adult and the young stem is the presence of a layer of "tangential cells" outside the metaphloem region of the meristele.

One or two features in which the adult differs from the young plant may be mentioned. The endodermis surrounding the meristeles is secondary in type and the endodermal cells do not contain the tanniniferous contents so characteristic of the endodermis of young plants. Another point of difference is the fact that it proved impossible to recognise the protophloem and protoxylem elements in the meristeles of the adult.

The medullary bundles are similar in structure to those of the young plant. They are amphicribral and the majority of

Cyathea contaminans (Wall.) Copel.

Dichotomously branched veins

Fig. 29/A. Part of a frond showing abaxial sori and open venation.

(x 4.)

them have a parenchymatous central region.

THE FROND

(a) External features. The plant from which the material was obtained is stated to have had 14, thorny, curved but stout leaves. The stipe and lamina of a leaf measured about 66 and 324 cm respectively. In the living condition, an interrupted green stripe was noted on the sides of both stipe and rachis, which is purple at maturity, and has thorns, doveloped from bases of scales. Often hairs and scales are found in great abundance on the rachis even at maturity. The pinnules, which often attain a length of 15.5 cm and breadth of 2 cm, have an acuminate apex and truncate base. The edges of the pinnules which are thin but firm, are slightly crenulate and have rounded apex. The venation is dichotomous (fig. 29/A). The sori are superficial and always circumscribed and are arranged in a row near costules, on either side. Fusions between adjacent sori were never found. There is no indusium, but, in rare cases, a reduced scale is present. Multicellular paraphyses occur among the sporangia.

(b) Anatomy of the rachis. In transverse section the rachis is oval. The single layered epidermis consists of living cells with their outer wall thick and cutinised. In longitudinal section these cells are much elongated. Thorns, hairs and setiferous scales are borne on the epidermis, which is often interrupted by the presence of pneumathodes. The hypodermis of the rachis is a sheath of sclerenchymatous fibres, 25 - 31 cells deep. Below the hypodermis, lies the fundamental parenchymatous tissue with intercellular spaces, and a number of mucilage sacs. The numerous pneumathodes, arranged in two rows down the sides of the rachis, provide a channel of aerenchyma through the sclerenchyma of the hypodermis (fig. 28).

Cyathea contaminans (Wall.) Copel.

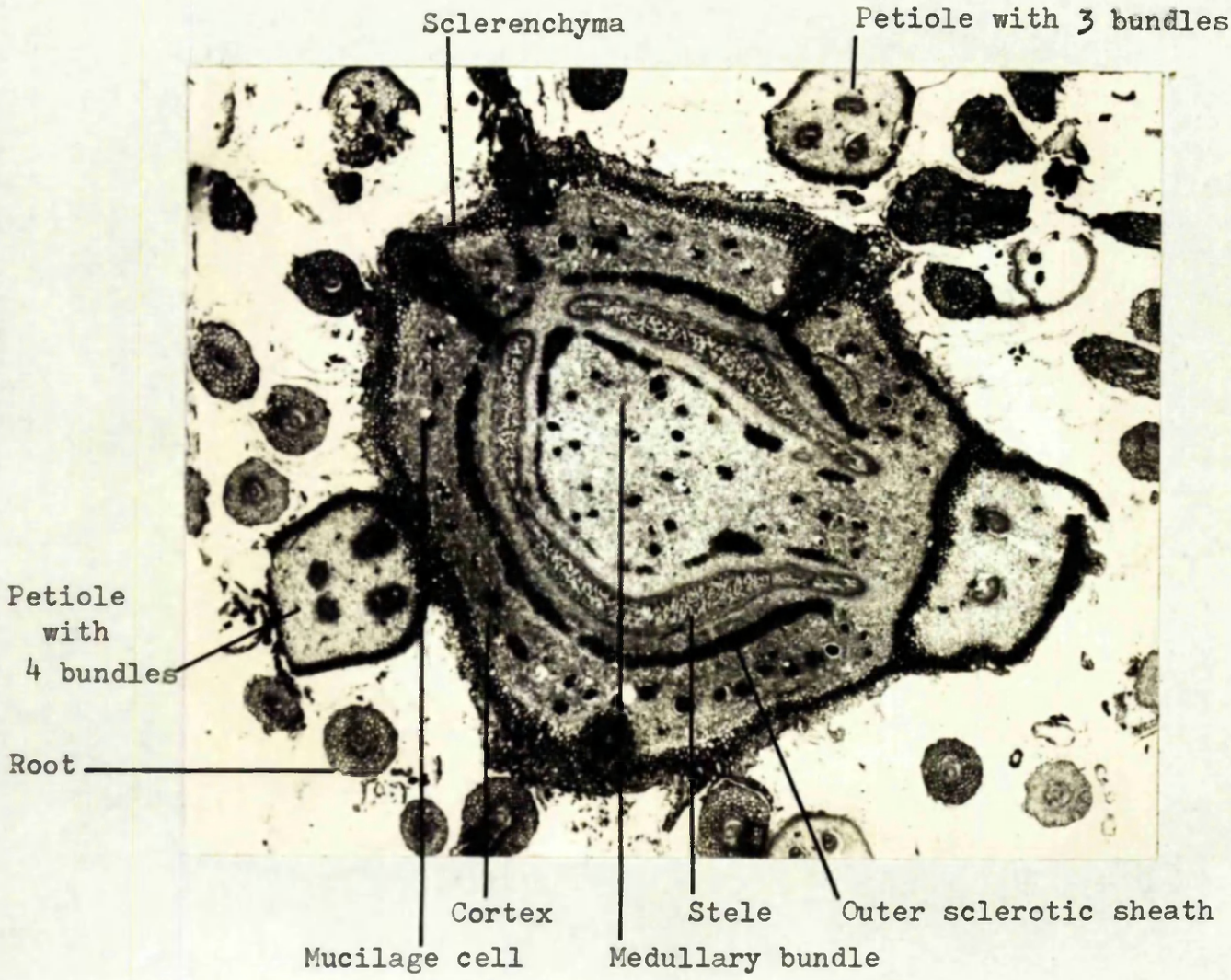


Fig. 30. Photograph of a transverse section of the stem. (x 9.)

The individual petiolar vascular strands, which may number 110 - 115 at the base of the frond, undergo lateral fusion in the rachis to form continuous ribbons; but the distinction between abaxial and adaxial series of strands is maintained (fig. 29).

Each corrugated ribbon may be regarded as a series of V- or W-shaped bundles united laterally. The detailed structure of each of these units is identical with that of a separate petiolar strand of a young plant (see fig. 16).

(c) Structure of the lamina. A transverse section through the lamina shows that the epidermis consists of a single layer of closely fitting cells, with outer walls thickened and cutinised. The mesophyll is not differentiated, but, as in the young leaf, it is more compact on the upper surface than on the lower. The traces are collateral in structure. The stomata are on the abaxial surface and resemble those of the young plant.

(d) The sporangia. The sporangia are borne on hemispherical receptacles in basipetal succession. They vary from .2 - .3 x .3 - .45 mm and have an oblique annulus, a poorly defined stomium and a short stalk. The spores are tetrahedral, and triangular in polar view. Their sides are concave and have rounded angles. The trilete mark is simple, and the rays extend almost to the equator. The exine, which is thin and measures about 1 u, is smooth. Mature spores are hyaline to slightly yellowish, and vary from 30 - 32 u in diameter.

Cyathea pulcherrima Copel.

Fig. 31

Fig. 32

Fig. 31. Part of the stem showing the arrangement of leaf-scars.
Fig. 32. A leaf-scar showing the arrangement of leaf-traces.
(31, nat. size; 32, x 4.)

Cyathea pulcherrima Copel.

Cyathea pulcherrima is a very graceful tree fern with horizontally spreading leaves. It often attains a height of 5-6 meters and is very abundant in sheltered moist hollows in the tall forests of the Cyclops Mountains in Netherland New Guinea.

ADULT PLANT

The material was collected in June, 1938, on the east slopes of the Cyclops Mountains, at an altitude of 575 meters. The material on which the following account is based came from a plant which had a stem measuring 3 cm below the crown of fronds. The latter were 5 in number, and were 150 - 160 cm in length including the stipes.

THE STEM

The stem is erect, unbranched and has spirally arranged leaf-scars with projecting leaf-traces showing typical cyathean arrangement (figs. 31, 32). The spaces between the scars are covered with rather thin, densely packed, deep brown, elongated scales, beneath which there is an extremely hard protective tissue. Pneumathodes, penetrating this sclerotic tissue, occur below each leaf-scar, protection against the entrance of parasitic organisms being given by the dense covering of scales. As in Cyathea contaminans, the leaf-scars are oval, and measure about 2.5 x 2 cm. About 41 - 43 leaf-traces projecting from a single scar show the characteristic arrangement. The two pairs of odd traces associated with the two adaxial groups, and the traces forming the inturned margins of the abaxial semicircle in the leaf-scars of Cyathea contaminans are, however, absent in this species.

Cyathea pulcherrima Copel.

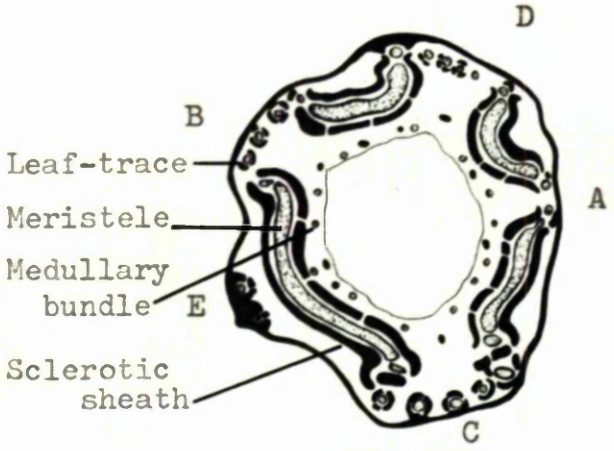


Fig. 33

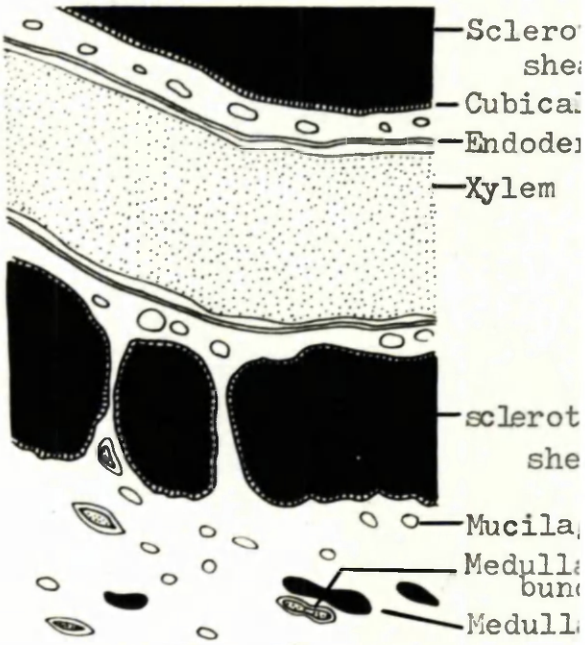


Fig. 34

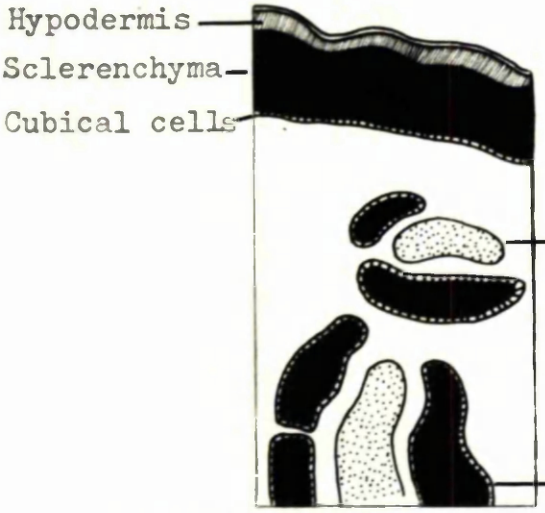


Fig. 35

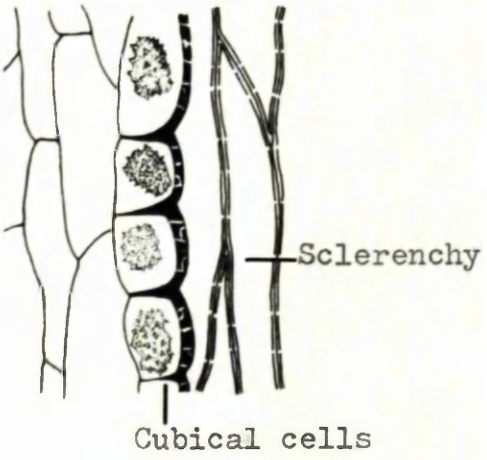


Fig. 36

Fig. 37

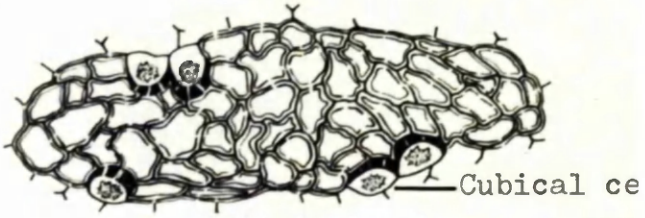


Fig. 38

Fig. 33. T.S. of the stem (A - E, position of leaf-gaps). Fig. 34. T.S. throu a meristele. Fig. 35. T.S. of the external part of the stem. Fig. 36. L.S. of part of the stem showing the transition between parenchyma and sclerenchyma. Fig. 37. A dissected leaf-gap: overlying sclerotic plate and parenchyma partially removed. Fig. 38. T.S. of a medullary sclerenchymatous strand. (33, x 1.5; 34, x 15; 35, x 13; 36, x 264; 37, x 2; 38, x 160.)

Anatomy

Anatomy Figure 33, which represents a transverse section of the stem, shows that the outline of the stem is more or less irregular. The peripheral hard tissue measuring about .5 mm in thickness, is dark brown in colour and surrounds a zone of white parenchyma, which is about .1 - 3 mm in thickness. The stele forms a discontinuous ring, about 2.3 cm in diameter, and is interrupted by 4 - 5 leaf-gaps. The meristeles are of uniform width except where the margins curve outwards. As a result of outward curving, the meristeles form flattened U-shaped structures. They are surrounded by a dark brown sclerenchymatous sheath varying in thickness from .7 - 1.5 mm. The outer sclerenchymatous sheath is a continuous layer, but the inner one is interrupted at intervals by parenchyma. The mode of departure of the leaf-traces can be followed in relation to the leaf-gaps which are cut across at varying levels (fig. 33). These traces, each surrounded by strands of sclerenchyma, are usually given off in pairs, one trace from each side of the gap. At A in fig. 33 is seen the lowest pair of leaf-traces given off from the base of a leaf-gap which has just opened; at E, the highest, i.e. the adaxial, traces are seen, the gap from which they departed having just closed. The gaps shown at B, C, and D and their related leaf-traces are cut across at intermediate levels.

Cortical bundles which have been found in certain spp. of Cyathea are absent in this species, as they are in C. contaminans. The central part of the stem is occupied by a pith about 1.7 cm in diameter. In this region numerous medullary bundles and isolated sclerenchymatous strands are present.

The cells of the epidermis are rather tubular and form

Cyathea pulcherrima Copel.

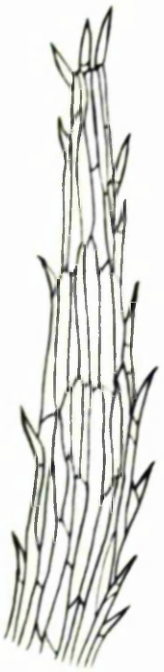


Fig. 39

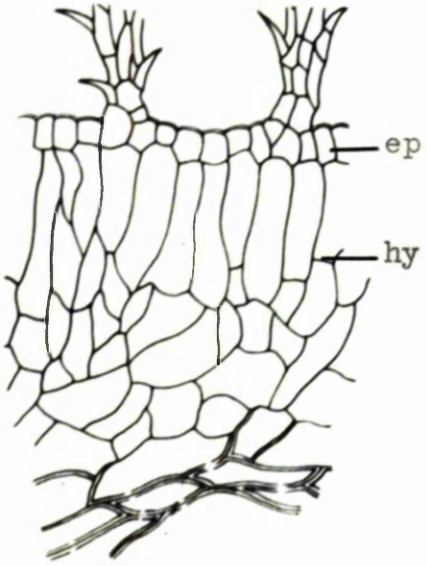


Fig. 40

Fig. 41

Fig. 42

Fig. 43

Fig. 44

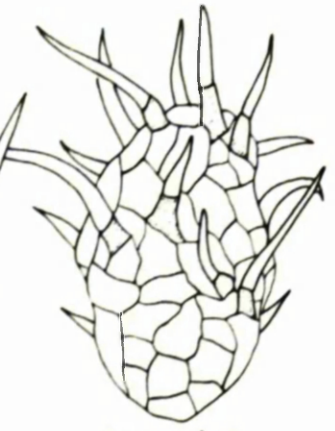


Fig. 45

Fig. 39. A setiferous scale. Fig. 40. T.S. of the external part of the cortex showing epidermis (ep), and hypodermis (hy). Fig. 41. A bristle with setiferous projections. Fig. 42. L.S. of a bristle. Fig. 43. Unbranched hair. Fig. 44. A setiferous scale. Fig. 45. An oval scale.

(39, x 17; 40, x 102; 41, x 21; 42, x 108; 43, x 21; 44, x 100; 45, x 100.

a continuous layer except at the lenticular openings. The outer wall of the epidermal cells are thickened and cutinised (fig. 40). At certain regions, the epidermis as it ages is peeled off, but in most of the regions it is persistent. The setiferous scales are the only epidermal appendages of the stem, and probably persist throughout the life of the plant. As in Cyathea contaminans, these scales are composed of much elongated cells with their long axes developing in the same direction as the length of the scale (fig. 39). The elongated cells are modified parenchyma with considerable thickening and irregularly distributed pits in their tangential walls. The setiform projections of the margin are also thick-walled, and dark brown in colour.

The hypodermis, which is composed of thick-walled parenchymatous cells, is about 4 - 10 cells deep. These cells are radially elongated, and gradually pass into the next fibrous layer, about 24 - 30 cells deep. The fibres are shortly elongate, and have pointed ends. The pits on their walls are simple and irregularly distributed. Due to great deposition of lignin, the lumen of these fibres often becomes very narrow. Internally this tissue ends abruptly, being lined by a layer of cubical cells with their characteristic inclusions (fig. 36). Well-developed pits are found on the thickened tangential walls of these cells. The zone inside the cubical cells is composed of parenchymatous cells with intercellular spaces. The leaf-traces, which are situated at the periphery of this tissue, are more or less reniform in outline, and have their discontinuous sheaths surrounded by a layer of cubical cells (fig. 35). Within the cells of this zone, numerous mucilage sacs, either isolated or in groups, are found. These sacs are oval to elliptical in longitudinal section, and often form blind, irregular rows due to the breaking down of the common walls of two or more

adjoining sacs. The fibres lying inside the parenchymatous zone, and forming the outer protective sheath of the vascular tissue, are extremely hard and are more elongated (often attaining .99 mm) than those comprising the inner layer of the peripheral protective tissue of the stem. The outer protective sheath of the vascular tissue is surrounded by a continuous layer of cubical cells (fig. 34). The next inner layer of parenchymatous cells is very similar to the middle parenchymatous zone of the cortex. In this zone also mucilage sacs are found. The endodermis surrounding the meristeles is of secondary type. When the endodermal cells are treated with Methyl red, the well-developed casparian strips on their radial walls become red, while the thin suberine lamellae lining their inner tangential walls only, colour yellow. Lying internal to the endodermis, and ensheathing the vascular tissue, is the 1-2 cells deep parenchymatous pericycle. The protophloem layer is not evident, but in some sections an ill defined layer of crushed cells is found. Tangential cells are present next to the pericycle or the crushed layer of cells. They are very similar to those of Cyathea contaminans, but differ in that they lack the mucilaginous substances, which are occasionally found within the cells of the latter. The sieve cells of the phloem are variable in length, and often attain 20 u in width.

The xylem, which is separated from the phloem by the conjunctive parenchyma is composed of tracheids and paronchyma, vessels being absent. All tracheids in a mature plant show scalariform-pitted thickening, so that the position of the protoxylem cannot be ascertained. These tracheids are about 2.4 mm in length, and about 0.12 mm in bfeadth. The wall of a mature tracheid with its secondary thickening measures about 12.5 u in thickness.

The hollow pith can be divided into three layers: i. the first layer is parenchymatous, and is very similar in construction and thickness to the innermost cortical layer; ii. the second layer is a discontinuous sclerenchymatous sheath on the inside of the meristele (fig. 34), and is composed of extremely hard fibres. Each of the sclerenchymatous masses is surrounded by a typical layer of cubical cells; iii. the innermost layer of the pith is parenchymatous.

The medullary bundles, which appear elliptical in transverse section, have no sclerenchymatous sheaths, and structurally resemble those in C. contaminans. The tracheids of the metaxylem of a medullary bundle vary from .2 - .35 mm in length and 30 - 33 u in breadth, while their wall measures about 2.5 u in thickness. A medullary bundle either unites with a meristele of the outer ring, or directly passes into the petiole through a leaf-gap. At maturity a bundle often becomes .9 x .2 mm.

In transverse section medullary strands of sclerenchyma appear oval or elliptical (fig. 38). The peripheral layer of rather dark coloured fibres is often associated with cubical cells. Some strands have regularly distributed cubical cells, forming a distinct layer, while in others the cubical cells are isolated. As shown by longitudinal sections, these medullary strands form an anastomosing system. A fibre of a medullary strand measures about .3 mm in length and 30 u breadth, while its wall with irregularly distributed pits attains a thickness of 7 u.

Leaf-gap

In a section, parallel to the surface of the stem, a leaf-gap is fusiform and varies from 3 - 3.5 cm in length, and 1 - 1.7 cm in breadth at the widest part, which is about

1 cm from the top of the gap. The bottom .5 - 1 cm of the gap remains covered externally by the protective tissue of the stem, while the remaining part of it is covered by the hard sclerotic plate of the leaf-scar. Fig. 37 shows a dissected leaf-gap. The immediate overlying sclerotic plate and the parenchyma of the leaf-gap have been partially removed. This dissection shows two medullary bundles curving outwards through the parenchyma of the leaf-gap, and passing out into the petiole where they ultimately join with other members given off from the margins of the gap. Before emerging from the leaf-gap, they become laterally connected with the outwardly turned margins of the meristeles near the apex of the leaf-gap. This dissection also shows in the middle of the leaf-gap, another pair of medullary bundles separately uniting with another pair of traces given off from the margins of the gap to form a pair of combined strands.

THE LEAF

The more or less rhomboidal, tripinnate leaves have stout, dark to medium brown stipes often attaining a length of 60 cm. These stipes, with deep adaxial and lateral grooves are covered with a few hairs, and numerous radially projecting, stiff columnar bristles with setiform projections (fig. 41). The bristles are longitudinally ribbed and dark brown in colour. In cross section, they appear circular in outline, while in longitudinal section, they are seen to be composed of much elongated, thick-walled parenchymatous cells (fig. 42). At maturity these bristles attain a length of 2.3 cm.

The medium brown rachises, which often attain a length of 100 cm, are similarly channeled on the adaxial and on lateral sides, and are covered with columnar setiferous bristles, and almost equally frequent unbranched hairs

Cyathea pulcherrima Copel.

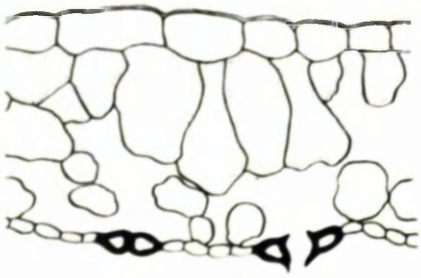


Fig. 46

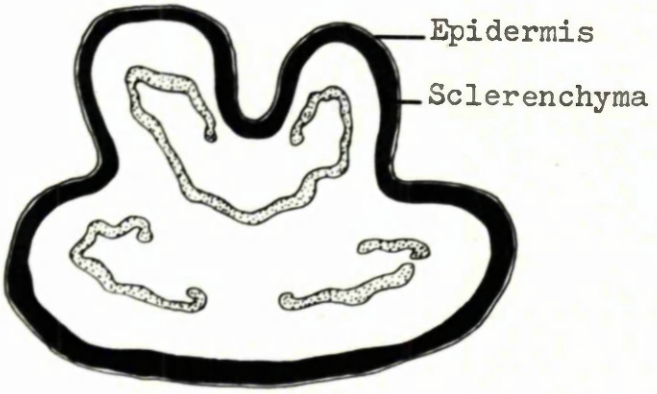


Fig. 47

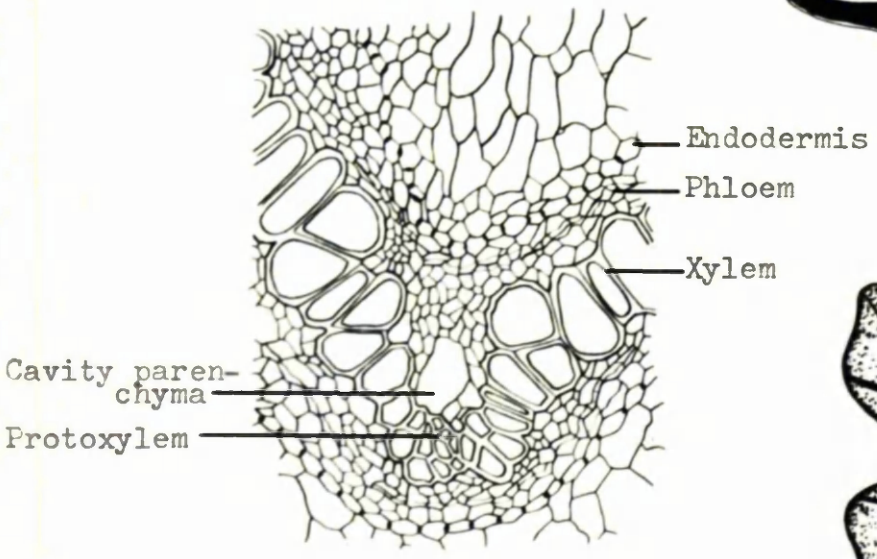


Fig. 48

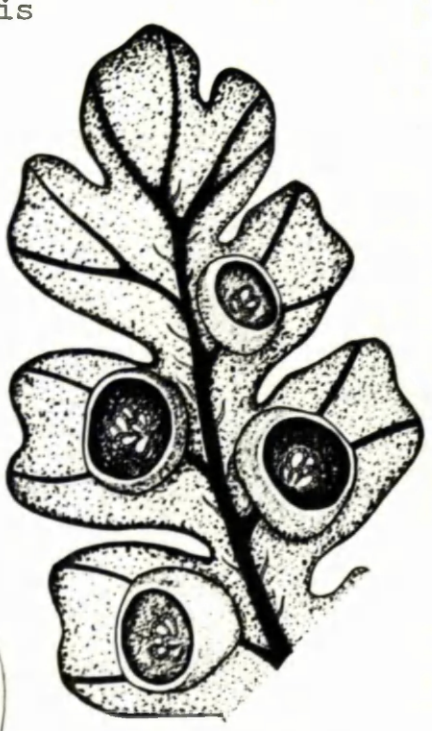


Fig. 50

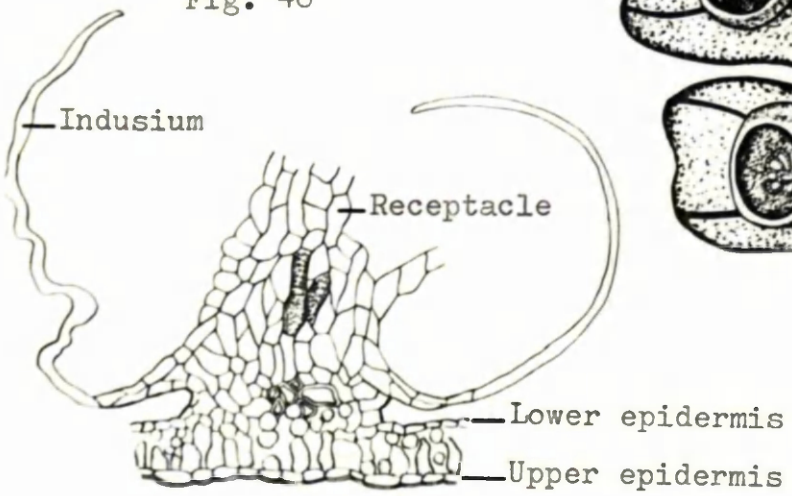


Fig. 49

Fig. 46. T.S. of a part of lamina. Fig. 47. T.S. of the rachis. Fig. 48. T.S. of a part of a petiole. Fig.49. Vertical section of a receptacle. Fig. 50. Part of a frond showing the sori on the abaxial surface.
(46, x 162; 47, x 5; 48, x 200; 49, x 108; 50, x 6.)

(fig. 43), white to pale yellow in colour. Intermingled with these bristles and hairs, there occurs another type of scale, which consists of an oval mass of parenchymatous cells with laterally projecting setae (fig. 45). The mass of cells is white in colour, whereas their setiform projections are dark brown. It seems that these "oval scales" have developed by modification of flat setiferous scales.

The pinnae, which are borne more or less at right angles to the rachis, often attain a length of 50 cm, and a breadth of 18.3 cm. They are medium brown, and are provided with stalks 2 mm to 1 cm in length. On both surfaces of the pinnae, but only over the veins, numerous hairs, "oval scales" and few setiferous scales (fig. 44) are found. The pinnules, which are about 9 cm by 2.2 cm, are shortly stalked and are borne in about 34 pairs, though the pairs on either side of the pinna are not exactly opposite. The pinnules of the second order are pinnatifid.

T.S. of the rachis

In transverse section the outline of the rachis is almost oval with one adaxial and two lateral indentations (fig. 47). The single layered epidermis, is a continuous layer, except at the pneumathodes. In transverse section, the cells of this layer appear nearly isodiametric, and each cell bulges out a little on the surface of the rachis. There is a thin cuticle on the outside of these cells. On the epidermis are borne scales and hairs. Beneath the epidermis is a layer of brown thick-walled sclerenchyma, 15 or more cells deep. Below the hypodermal sclerenchyma lies the fundamental tissue of parenchymatous cells with intercellular spaces. Within this tissue mucilage sacs, similar to those of stem, are often found. The petiolar bundles within the rachis unite laterally with one another,

and form three or four groups of bundles, of which one is adaxial, and the remaining two or three groups of bundles are abaxial (fig. 47). The detailed structure of a petiolar bundle is more or less similar to that of C. contaminans. However, the mucilage cells, which were found associated with the phloem of C. contaminans, are absent in this species (fig. 48).

The pneumathodes, which break the continuity of the epidermis, consist of very loosely arranged thick-walled cells of the hypodermis, and communicate with the exterior by means of an opening, resulting from the death of one or more epidermal cells. It is not certain whether at the early stages of development, the aerenchyma is covered by an epidermis with stomata.

Structure of the lamina

At the upper surface of the lamina there is an unbroken epidermis of wavy margined cells with a thin cuticle (fig. 46). Over the veins, the epidermal cells are elongated and rectangular, while elsewhere, they are very wavy in surface view. Many oval stomata, about 42.5 x 25 u, break the continuity of the lower epidermis. There are about 148 of them per square mm. They are set at a level slightly higher than the neighbouring cells, and they have ledges of cutinised wall material appearing as horns in a section. The cells of the lower epidermis are smaller and more wavy than those of the adaxial surface. The thickness of the lamina varies from 1 mm at the veins to .2 mm where the mesophyll cells are well developed. On the adaxial side, the mesophyll cells form an almost continuous layer of palisade-like cells. The air spaces in the abaxial half of the spongy parenchyma are large. The veins of the fronds are collateral.

SORI AND SPORANGIA

The receptacle

The elevated, oval to hemispherical sporangial-receptacles are borne on the abaxial surface of the fronds, where the lateral veins bifurcate (fig. 50). Scalariform and a few annular tracheids supply these receptacles (fig. 49). The membranous indusia, which are 1-cell thick, are saucer-shaped, and are attached at the base of the receptacles.

The sporangia

The sporangia are club-shaped with short and stout pedicels. They vary from .45 - .49 x .25 - .35 mm. The annulus is oblique enough to pass the pedicel.

The spores

The spores are tetrahedral, anisopolar and yellowish in colour. They are triangular in polar view with concave sides and broadly rounded angles. The trilete mark is conspicuous, and the rays almost reach the equator. The exine varies from 1 - 1.5 u in thickness, and is spiny. The spines are soft, and extend up to 3 u. Mature spores measure from 50 - 56 u.

Cyathea orientalis Moore.

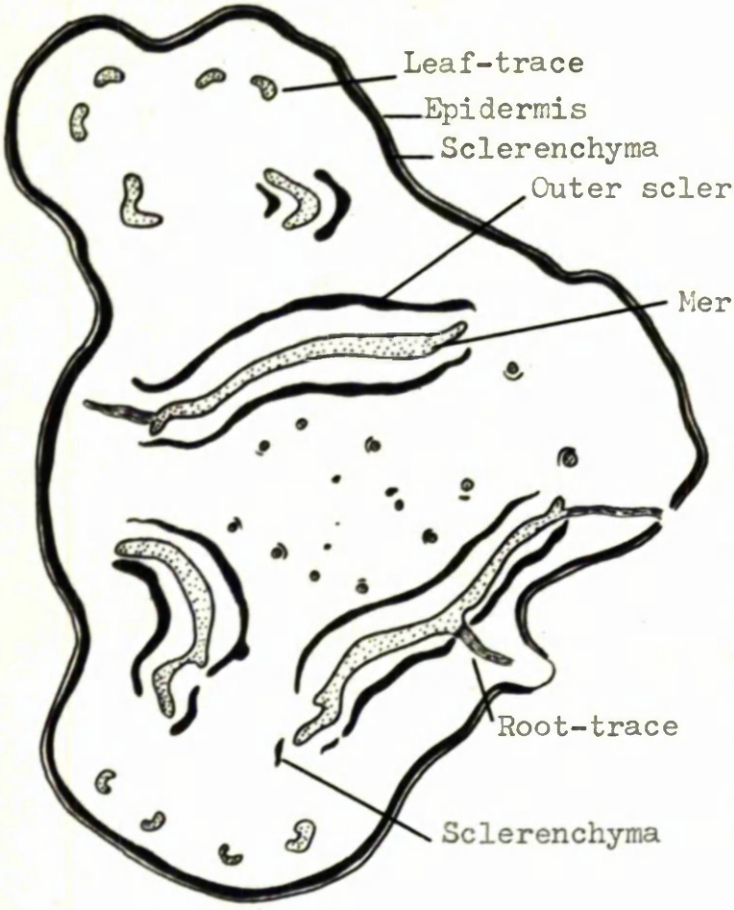


Fig. 51

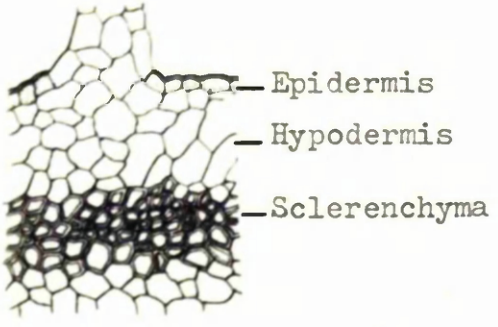


Fig. 52

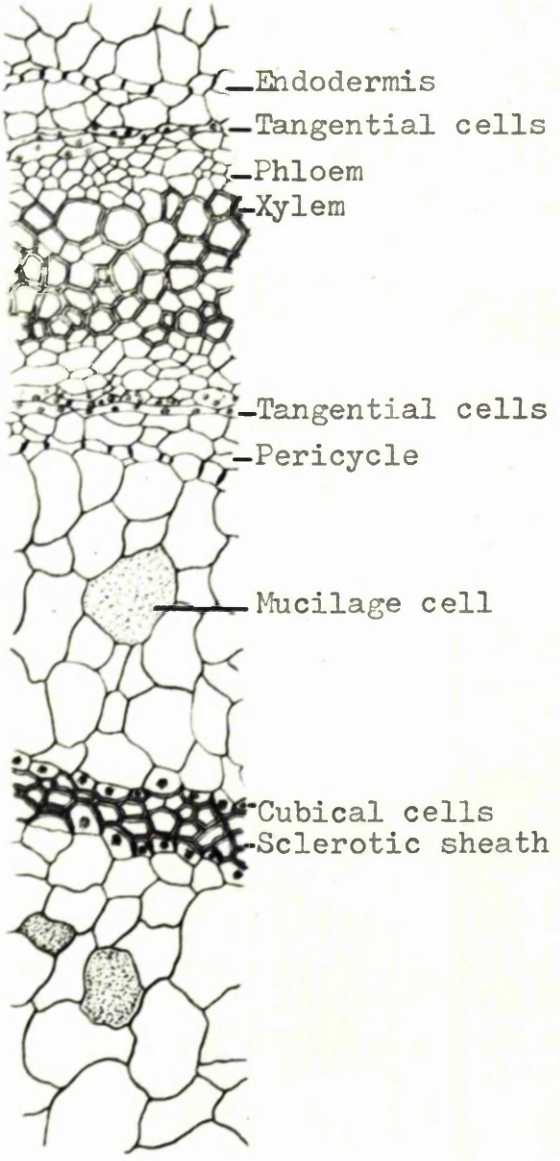


Fig. 53

Fig. 51. T.S. of the stem. Fig. 52. T.S. of the peripheral part of the stem.
Fig. 53. T.S. of the inner part of the stem.
(51, x 10; 52 and 53, x 108.)

Cyathea orientalis Moore.

Much of the anatomy of Cyathea orientalis, which is an inhabitant of Java, resembles that described above for Cyathea contaminans. Only features of particular significance are described here.

YOUNG PLANT

The following description is based on a single plant, collected in July 1959, from the Royal Botanic Garden, Kew.

THE STEM

The material examined had a stem about 2.5 cm in length and 1 cm in diameter. Figure 51 shows the general anatomical structure of the stem, while figs. 52 and 53 show its detailed histology.

The epidermis consists of short cells with a cuticle, which has a smooth outer surface. The only epidermal appendages of the stem are scales of a characteristic structure; they form a thick coating over the surface of the stem. The scales are flat and consist of a central zone of thick-walled, dark coloured cells and margins of thin-walled cells. The central zone, which consists of cells elongated in the long axis of the scale, tapers at the distal end of the scale and terminates in a stout seta. The thin-walled elongated cells of the wings diverge from the central regions in a fan like fashion and terminate in short celled projections, thus giving a lacerate margin (fig. 54). Narrow setae are also developed from some of the marginal cells. Prof. Holttum (1957), found a similar type of scale in Gymnosphaera glabra and some other species of Cyathea, and proposed the term flabelloid for this type of scale. The lateral setae projecting from the scale margins have been noted only amongst the Cyatheaceae (sens. str.) e.g., on small scales borne on the costae of Cyathea kingii and on stipe

Cyathea orientalis Moore.

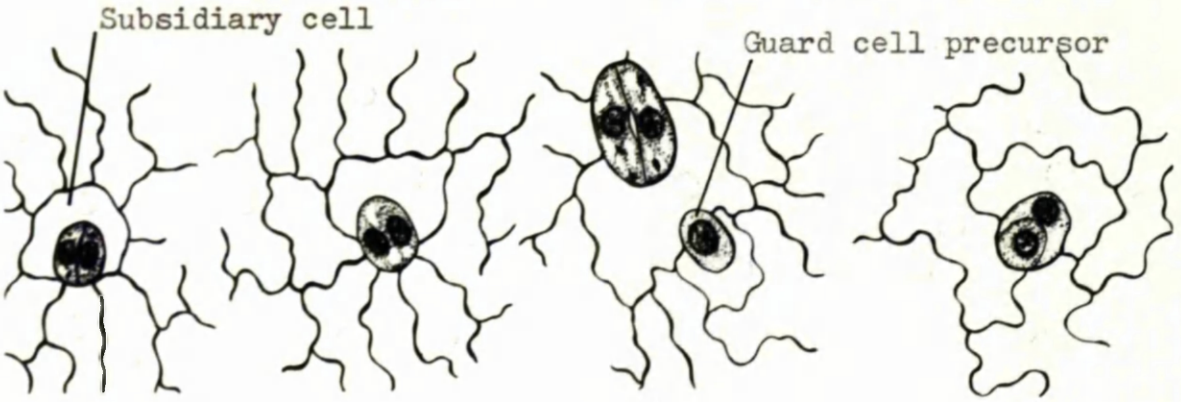


Fig. 58

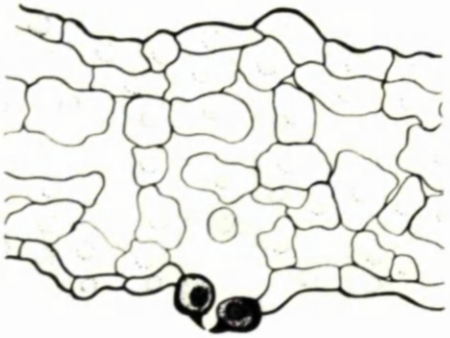


Fig. 57

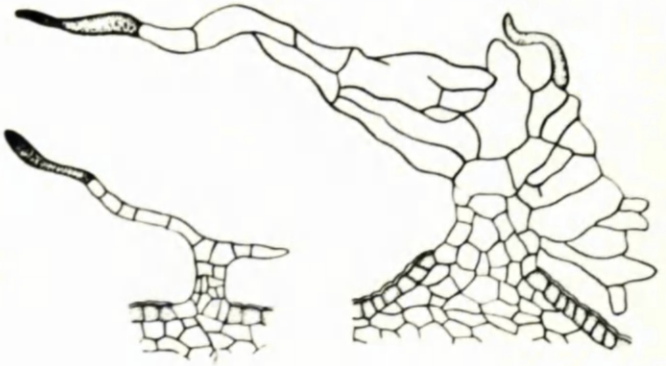


Fig. 56

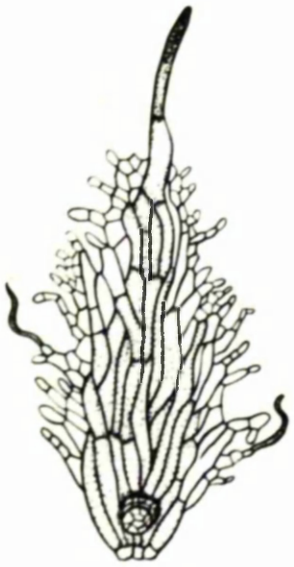


Fig. 54

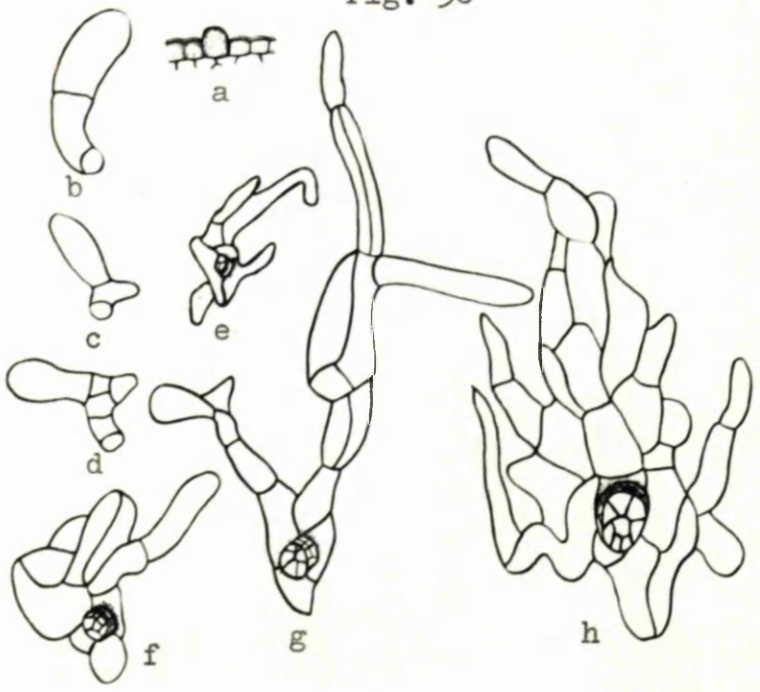


Fig. 55

Fig. 54. A flabelloid scale. Fig. 55. Stages in the development of the scales showing uniseriate peltate condition during ontogeny. Fig. 56. L.S. of flabelloid scales showing peltate base. Fig. 57. T.S. of a part of lamina. Fig. 58. Stages in the development of stomata.

(54, 55 b-h, 56, x 50; 55 a, x 80; 57, x 170; 58, x 350.)

scales of Cyathea latibrosa (Holttum, 1957).

Development of flabelloid scales

The developmental stages of flabelloid scales are shown in figs. 55, 56 . An initial cell first divides into an inner and outer cell. The inner cell bulges out laterally and elongates to form a peltate hair (figs. 55c, d). The newly projecting arm of the peltate hair is then cut off from the inner cell. The third division is transverse, and divides the inner cell into two cells which then undergo repeated transverse and longitudinal divisions and form the stalk of the scale proper. The two arms of the peltate hair undergo divisions in all directions, all the divisions being anticlinal, so that the scale remains one cell in thickness. The short marginal cells of the flat structure, derived from the arms of the peltate hair, radiate from their neighbouring elongated cells to give a lacerate margin. The setiform projections develop by modification of some of the marginal cells, and also of the tip cell. The thickening of the walls of the central cells takes place at a late stage of development.

The hypodermal tissue of the stem is parenchymatous, and is very variable in thickness. No mucilage sacs are evident in this layer (fig. 52). The next fibrous layer is also variable in thickness, and is limited internally by a layer of cubical cells. The cubical cells, however, form a definite layer on either side of the inner and outer smooth-margined, sclerotic sheaths of the vascular tissue (fig. 53).

Development of cubical cells

The cubical cells, which are differentiated in the ground meristem, and also in the procambial tissue, are recognisable even in the very early stages of their development, when no appreciable thickening has taken place in their walls. Over the primary cellulose wall, which

stains with iodine after treatment with sulphuric acid, there is a gradual deposition of secondary wall material. In the case of radial walls, and also three tangential walls, the secondary wall material consists of both cellulose and lignin, but it consists only of cellulose in the case of the other tangential wall of the cubical cells. The characteristic cell inclusions are visible soon after the differentiation of these cells. At early stages, the nuclei of these cells are very active, but in the later stages of development they disappear.

The third and the fifth layers of the cortex are parenchymatous and contain mucilage sacs.

The stele, even at the apparent base of the stem is solenostelic, but it gradually passes into a typical cyathean dictyostele. The individual meristeles are similar to those of Cyathea contaminans. The endodermal cells, apart from their characteristic lignin-suberin deposition, are recognisable by their contents. The parenchymatous pericycle is 1-2 cells deep. The protophloem layer is not evident. The tangential cells form a definite layer, 2-6 cells in thickness.

Development of tangential cells

The tangential cells differentiate within the cells of the procambium. During early stages of development, these cells are more or less cubical in appearance. They gradually elongate tangentially, and undergo a profound change during ontogeny. Their nuclei, which are very prominent during the early stages, gradually disintegrate, but thickening of their walls still continues. Sieve areas occur between vertically and laterally contiguous cells. Thus the developmental stages of these cells are very similar to those of the sieve cells of the phloem.

The tracheids of the xylem are of the scalariform-pitted type, and the pith, as usual, is differentiated into three regions. The medullary bundles originate de novo from the cells of the pith, and no bundles have been found to originate as internal projections of the meristeles. Some of these bundles are without any accompanying sclerotic sheath, while in others the sheath may occupy about half of their entire circumference.

THE FRONDS

The tri-pinnate fronds are spirally arranged, and their petioles are dark brown in colour. Numerous scales together with a few hairs occur on the petiole, but the hairs become dense over the rachis. The hairs are usually unbranched, but occasionally they may be branched. The pneumathodes are arranged on either side of the petiole and rachis, but they never form a continuous row. The primary pinnae are not strictly at right angles to the rachis, but are slightly inclined. The secondary pinnae, however, are borne almost at right angles to the primary ones. The ultimate pinnules are sessile, and oblong-lanceolate. The lamina is coriaceous, and is black-green, but paler beneath. The veins are free, and may be branched or unbranched.

Anatomy

The anatomical details of the petiole are almost identical to those of Cyathea contaminans. The main difference is that the epidermis covering the pneumathodes possesses stomata, which are persistent throughout, at least in the young plants. The ventilating tissue consists of very loosely arranged aerenchyma with a mass of sclerenchymatous tissue beneath. The aerenchymatous cells of the ventilating tissue are usually oval to elongate, and they are unique in having numerous lignified peg-like projections on their walls.

Cyathea costalisora Copel.

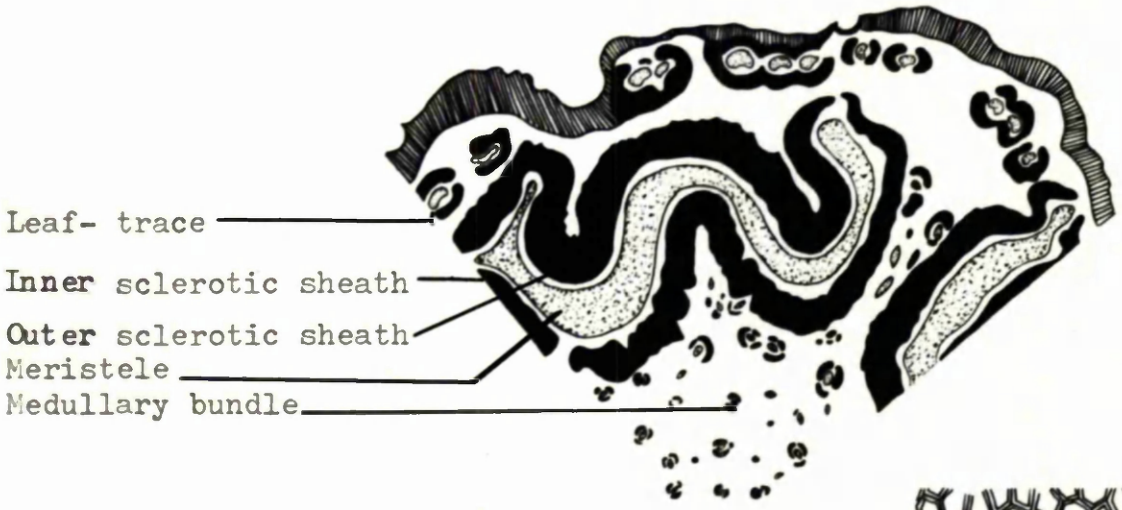


Fig. 60.

Fig. 59

Fig. 62

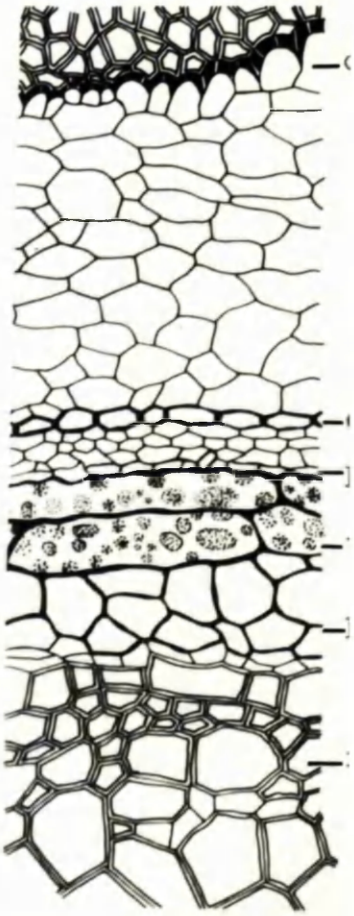


Fig. 61.

Fig. 59. T.S. of the stem. Fig. 60. Part of the transverse section of the ste
Fig. 61. T.S. of the inner part of the stem showing cubical cells (cc), endodermis (en), protophloem (pp), tangential cells (ts), phloem (ph), xylem (xy). Fig. 62. T.S. of a medullary bundle showing phloem (ph), xylem (xy).
(59, x 3/5; 60, x 5; 61, x 102; 62, x 55.)

Cyathea costalisora Copel.

ADULT PLANT

C. costalisora is one of the tree-ferns with an occasional distribution in the forests of moist hollows of Dutch New-Guinea. This fern attains the maximum height of 4 meters, and branches from near the base. The material for the present study was obtained from a branch having a diameter of 6 cm below the fronds, which were 9 in number.

The stem

The leaf-scars, which are arranged in a very close spiral on the stem, are circular to oval in outline, and have a diameter of 2-2.3 cm. The vertical distance between two scars varies from 1-1.5 cm, while the horizontal distance between them is 0.7 - 1.1 cm. As in C. pulcherrima, the adaxial leaf-traces, projecting through these scars, form shape, and there is no odd bundle between them. The number of these traces varies from 24 - 26. The abaxial bundles, about 22 in number, form a semicircle with incurved margins and thus resemble the abaxial group of C. contaminans.

Anatomy

The general distribution of tissues is similar to that described above for other species (figs. 59, 60).

The epidermis bears peltate, flabelloid scales. These are remarkable in having superficial as well as marginal thick-walled unicellular hairs. These superficial hairs resemble the single terminal cell at the tip of the central band of thick-walled cells. It may be noted that this terminal cell may occasionally be branched (fig. 64). The presence of superficial hairs on scales is an unusual feature in the ferns, but they are of universal occurrence in Tholypteris and in some species of Cyathea.

The cortex shows the same zonation as previously described species. Cubical cells occur round the sclerenchymatous sheaths of the leaf-traces and round the outer vascular sheath. Mucilage sacs in groups, or, very rarely, singly, occur in the parenchymatous zones.

The dictyostele shows 7-8 meristeles and, in relation to the intervening leaf-gaps, the origin and outward passage of the leaf-traces can be traced. Numerous medullary bundles, each associated with an incomplete cylinder of sclerenchyma, are present. The structure of the vascular tissue is very similar to that of C. contaminans. The protophloem forms a definite layer outside the layer of tangential cells (fig. 61). These latter do not show any mucilaginous content and, like the sieve cells of the metaphloem, they are rather thick-walled. The medullary bundles in the outer region of the pith are larger and more numerous than those occupying a more central position. The bundles are mostly accompanied by 2-3 strands of sclerenchyma, each of which is surrounded by a layer of cubical cells (fig. 62).

The medulla, as in species previously described, shows three zones. The only noteworthy feature is the presence in the central parenchyma of large aggregations of mucilage cells. No such aggregations were noted in either Cyathea contaminans or C. pulcherrima.

THE FROND

The stout stipe, which is medium brown in colour, measures about 25 cm in length and is densely covered with scales. The scales near the base of the stipe are large but they gradually become smaller and narrower towards the rachis. A scale situated near the stipe measures about 2.8 cm in length and 1.5 cm in breadth. The rachises are also medium brown and densely scaly. Between the scales are found multicellular, unbranched, pale hairs. The largest pinna is

Cyathea costalisora Copel.

Fig. 63. Part of a frond showing sori on the abaxial surface and flabelloid scales. (x 7.)

about 22 by 8 cm, and is borne almost at right angles to the rachis. Unbranched appressed hairs associated with scales are found on the adaxial side of the pinna rachises, while on the abaxial side, only scales, very rarely intermingled with a few hairs, are present (fig. 63). The penultimate segments are pinnatisect. The pinnules, which are adnate, are about 3 by 1 mm. On the adaxial side of the costa appressed hairs are found, while the abaxial side appears glabrous. The sori are found on both sides of the costa. They are in fact borne in pairs on either side of the costules and on the first pair of veins. Sometimes the second pair of veins also produce sori. The indusia are cup-shaped, and completely surround the sporangia in the young stage.

THE SPORANGIA AND SPORES

The club-shaped sporangia have stout stalks, and vary from .23 mm to .3 mm in length and 80 - 90 u in breadth.

The spores are anisopolar, triangular and have straight to slightly convex sides. The trilete mark is clear with simple rays reaching the equator; the angles are bluntly pointed. Exine is smooth, pale-yellow, and about 1 u thick. The mature spores are about 35 u across.

Adaxial surface

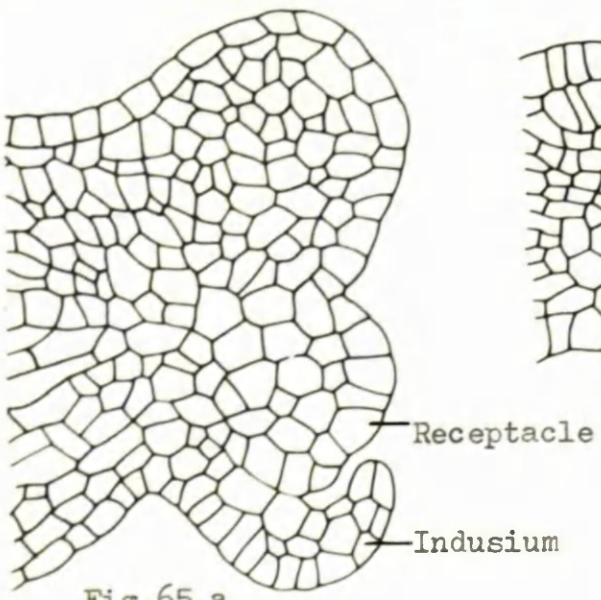


Fig.65,a

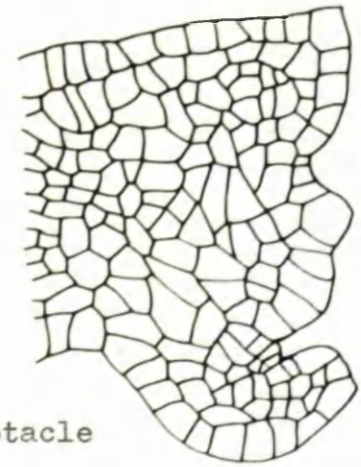


Fig. 65,b

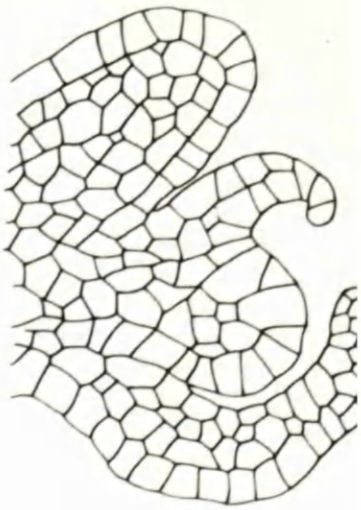


Fig. 65,c

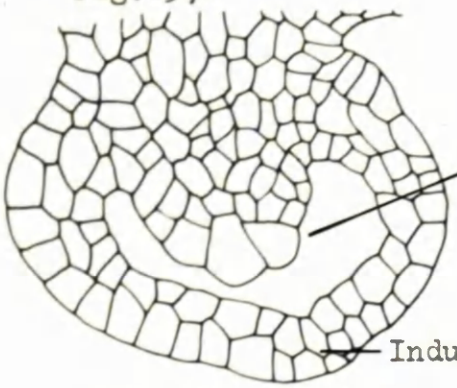


Fig. 65,d

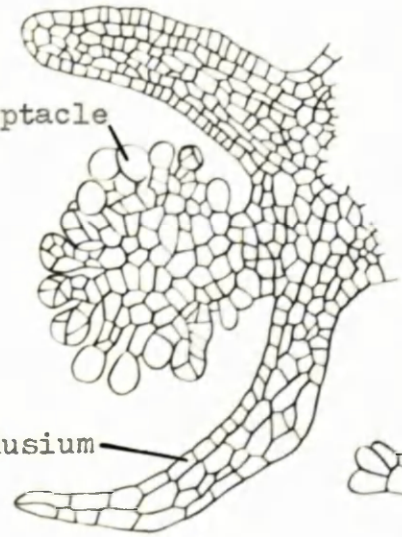


Fig. 66,a

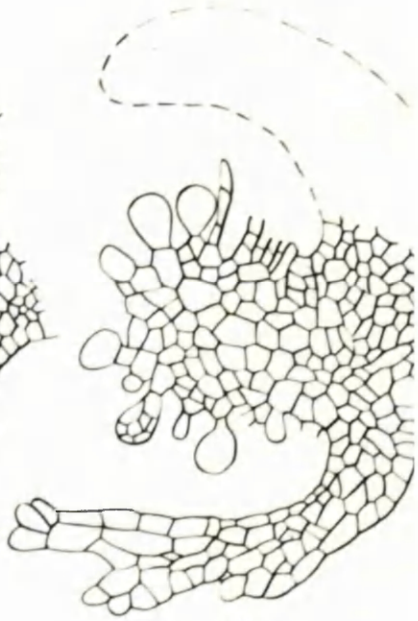


Fig. 66,b

Fig. 64,b

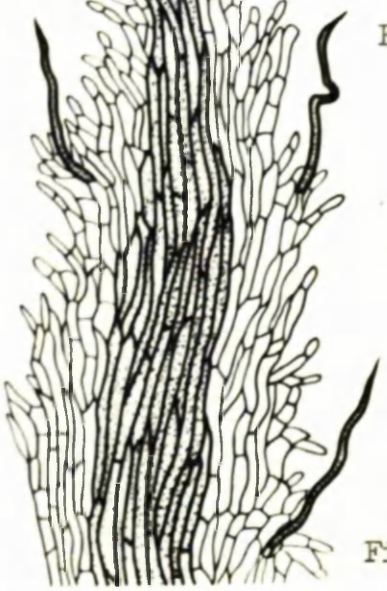


Fig. 64,a

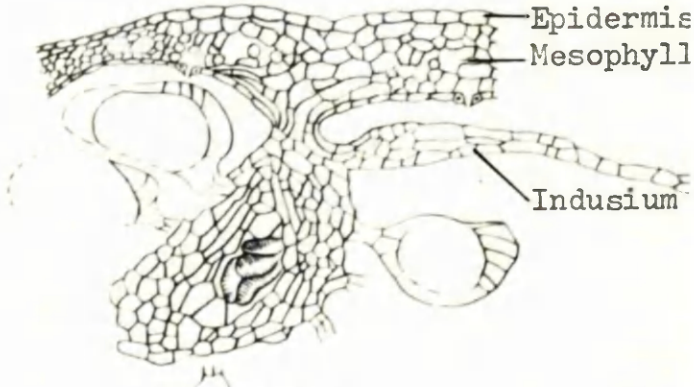


Fig. 66,c

Fig. 64,a. Cyathea **costalisora**. A flabelloid scale. Fig. 64,b. C. **costalisora**. A terminal cell of a flabelloid scale. Fig. 65. C. dealbata. Stages in the development of indusia in V.S. Fig. 66. C. capensis. Stages in the development of indusia. (64, x 50; 65, x 250; 66, a-b, x 120; 66,c, x 85.)

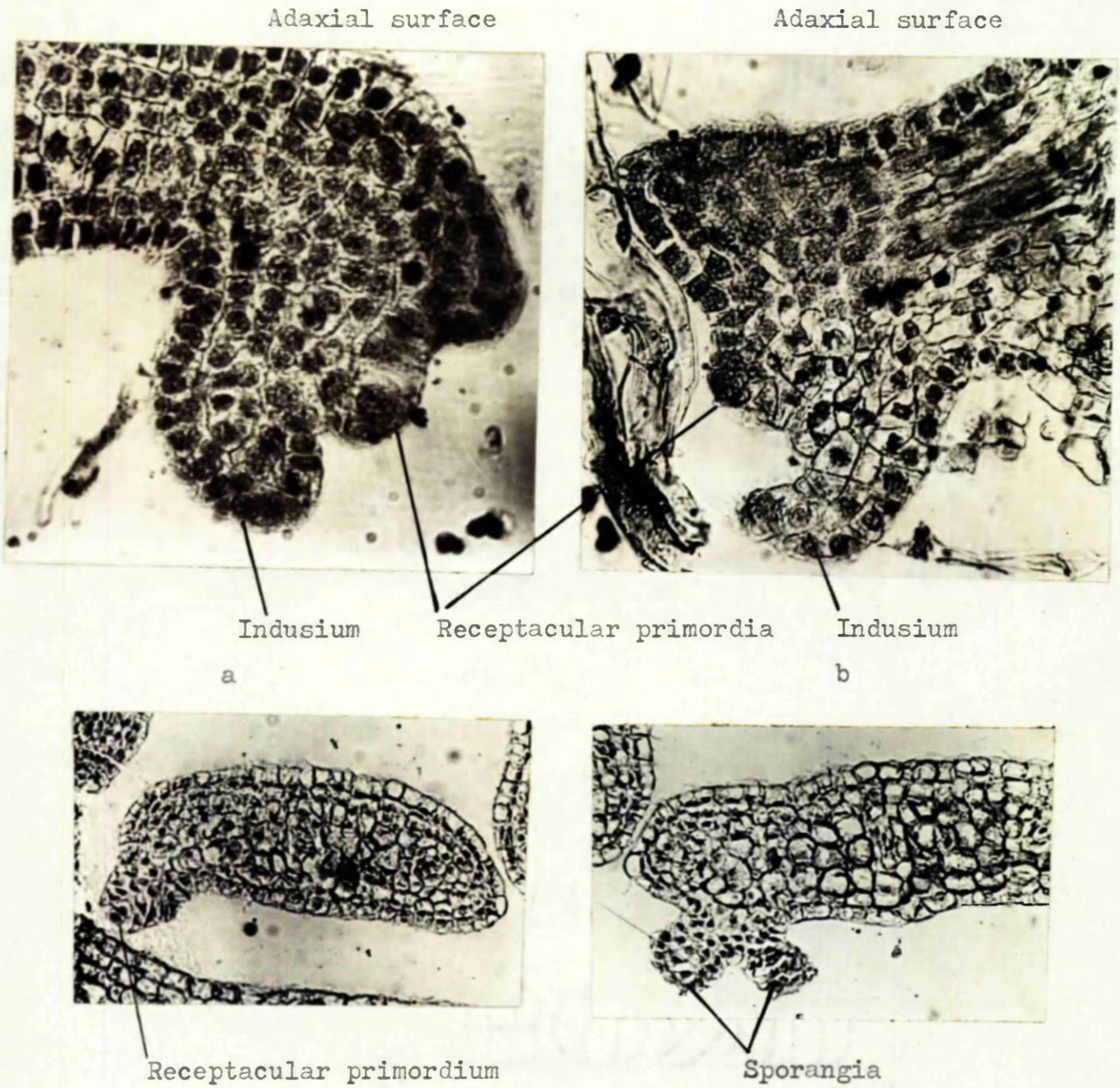


Fig. 66/A. Photographs from slides of Professor F.O. Bower.
a, Cibotium schiedei. Vertical section of a young sorus.
b, Cyathea dealbata. Vertical section of a young sorus.
c, Gleichenia sp. T.S. of a young lamina showing the inception of the receptacle on the margin, but very close to the abaxial surface.
d, Gleichenia sp. T.S. of a comparatively mature lamina showing the abaxial position of the sporangia due to growth of the marginal tissue.

(All, x 55.)

DEVELOPMENT OF THE SORUS IN CYATHEA

The development of the sorus was studied in Cyathea dealbata. In this sp., the mature sori are borne on the abaxial surface of the frond. The receptacle is more or less hemispherical, and it bears sporangia in strict basipetal succession. The sporangia are protected by a cup-like indusium.

Early stages in the development of the sorus can be studied in the still tightly circinate pinnule. At first the margin of the embryonic pinnule becomes more or less flattened, and soon it becomes, as seen in a vertical section of leaf, a three-lobed structure (fig. 65,a). The adaxial lobe forms what appears to be a continuation of the lamina, and develops at a much faster rate than the other two lobes (fig. 65,b). The middle lobe quickly becomes conical in form and ultimately develops into the receptacle. Any superficial cell of the receptacle may develop into an initial cell, which may give rise to a sporangium by oblique segmentations, or may develop into a thin hair. Bower (1899), has described the position of this receptacle as superficial from the very initiation, but during early stages it seems that at least, in certain cases, the initiation of the receptacle takes place at the margin (fig. 66/A,b), and that at this stage the young fertile frond is closely similar to that of Cibotium scheidei, in which the initiation of the receptacle has been described by Bower (1899) as strictly marginal. Of course, due to very rapid rate of growth of the adaxial lobe, the receptacle very soon appears as superficial in position. The abaxial lobe soon after its differentiation appears as a mere flap, but by subsequent elaboration it develops into the indusium. As the frond ages, the indusium extends laterally and forms a saucer-like structure (figs. 65, b and c), which later becomes

cup-shaped and eventually overarches the hemispherical receptacle (fig. 65, d).

Fig. 66, c, shows a transverse section of part of a fertile frond of Cyathea capensis. The receptacle, which is supplied with vascular tissue, is more or less circular and bears an inferior scale-like indusium of variable thickness.

In some examples the flap-like indusium terminates in a number of hair-like segments (fig. 66, b).

SUMMARY

1. The stems bear either setiferous or flabelloid scales; the former develop from simple hairs, the latter from peltate ones. In no species do both these types occur together. However, other types of scale may occur in addition to either the setiferous or the flabelloid ones. For instance, oval scales and stout bristles occur in Cyathea pulcherrima.

2. The stem is dictyostelic, and always has numerous medullary bundles. The meristeles are always protected by sclerotic sheaths, but the medullary bundles may or may not be protected by such sheaths.

3. Cubical cells with characteristic inclusions are present in the pith, and also in the cortex. They generally form a single layer round masses of sclerenchyma.

4. Tangential cells are always associated with phloem; they may or may not contain mucilage.

5. Mucilage sacs are present in the stem and also in the petiole. But they are not always present in association with the phloem of the petiole.

6. Numerous vascular strands are present in the petiole, and they form typical 7 shape. Scales and hairs which may be branched or unbranched, also protect the young petioles.

7. Sori, when mature, are abaxial in position.

8. Even where the indusium is a complete cup at maturity, it develops from a simple flap-like structure, and is inferior on a round to hemispherical receptacle.

9. The sporangia always show an oblique annulus and lateral dehiscence, and the spores are tetrahedral with trilete mark. The exine of the spores may be smooth or spiny.

10. Each of the stomata on the abaxial side of the leaves is usually surrounded by a single epidermal cell, and the wall separating the guard-cell mother-cell from its sister cell (i.e. the subsidiary cell) is almost elliptical.

Dicksonia L'Heritier (1788).

Introduction

The members of this genus are arborescent. Both stem and stipes are densely covered with simple hairs, scales being absent. The tripinnate fronds are usually rhomboidal in outline, and are large in size. The ultimate pinnules are dimorphic, the lamina of the fertile ones being slightly contracted or wanting. The costae of the ultimate pinnules are raised on the adaxial surface, and the veins are free.

The sorus is marginal and is borne on a single vein. The receptacle is flat and develops sporangia in basipetal succession. The latter are protected by a bi-valvate indusium: the upper valve is very similar to the lamina, while the lower one is hard and different from it. The sporangia may be long-stalked and have a conspicuous oblique annulus. The spores are tetrahedral.

There are about 17 species in the southern hemisphere (Christensen, 1938).

Dicksonia squarrosa Sw.

D. squarrosa is a tree fern of New Zealand, and Chatham Island. The small stem examined was 4.5 cm across, and was collected from New Zealand in 1925. Fronds were obtained from a plant, about 4.2 meters high, growing in the Botanic Garden, Glasgow.

THE STEM

The unbranched stem has a covering of old persistent leaf-bases. Many adventitious roots emerge from the petioles, but most of them fail to reach the soil and form a tangled

Dicksonia squarrosa Sw.

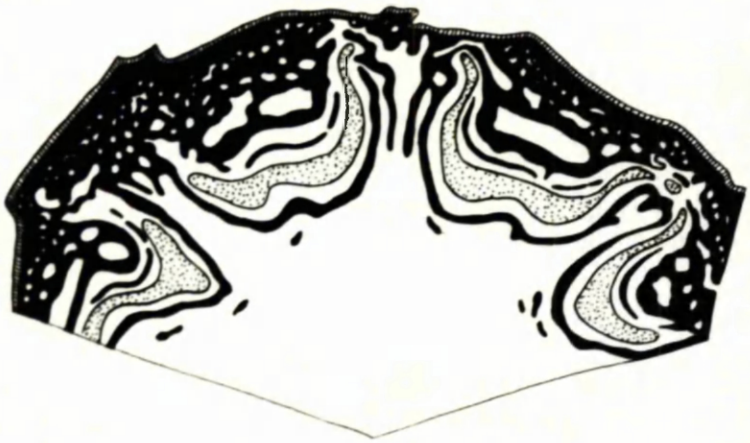
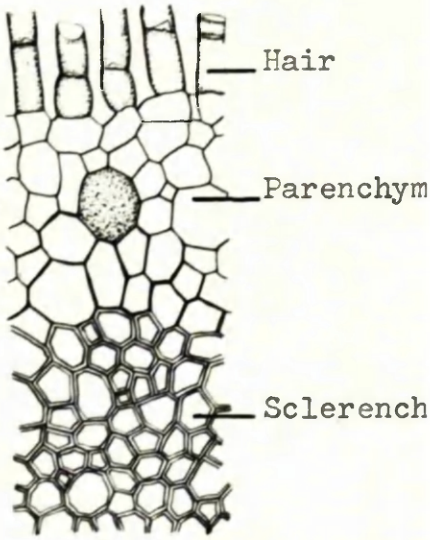


Fig. 67



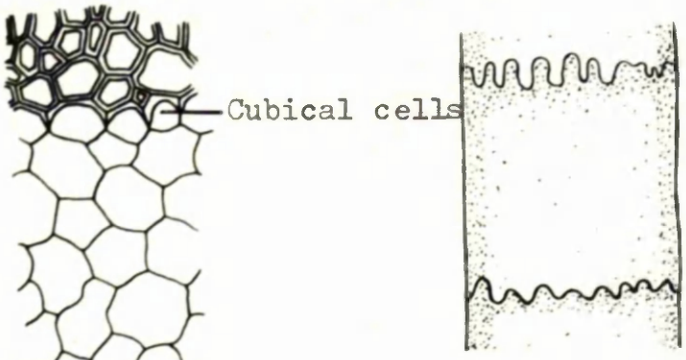


Fig. 71

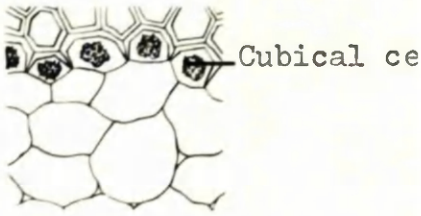


Fig. 68

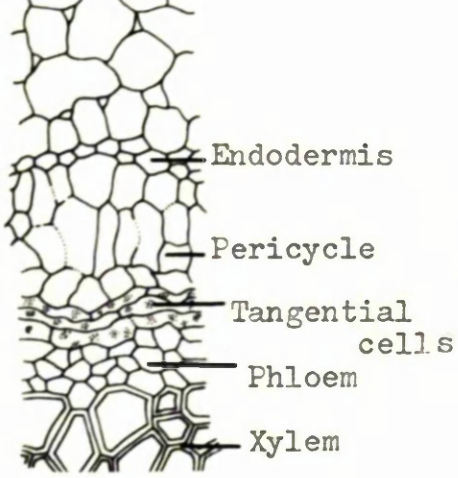


Fig. 69

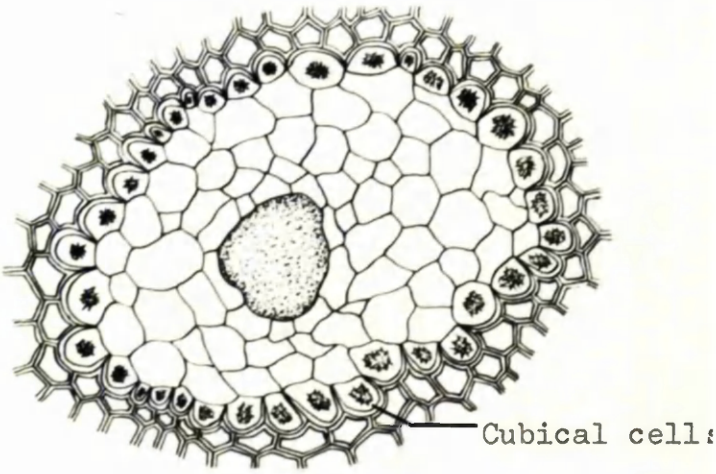


Fig. 70

Fig. 67. T.S. of stem. Fig. 68. T.S. of the peripheral part of the stem. Fig. 69. T.S. of the inner part of the stem. Fig. 70. T.S. of a mucilage sa within the peripheral tissue of the stem. Fig. 71. Part of an equisetoid hair. (67, x 2.5; 68, 69, x 132; 70, x 50; 71, x 150.)

mass over the stem.

The stem and petiole bases are clothed with simple uniseriate hairs which form a dense mass over the surface. The leaf-bases also bear dark coloured, much stouter and longer hairs seated on multicellular emergences. Both types of hair show the "equisetoid" condition resulting from frilling of the peripheral regions of the transverse septa (fig. 71).

Anatomy

The stem in cross section is nearly circular, but it has an irregular margin (fig. 67). The peripheral protective tissue, which is hard and brown in colour, varies from 2-6 mm in thickness. Within the peripheral tissue are found numerous irregularly arranged hyaline islets of soft tissue. Next to the peripheral zone is a hyaline layer of soft tissue about 1 mm in width. The corrugated vascular cylinder consists of 4-6 meristeles, which are either U or W-shaped structures, and are protected both externally and internally by bands of sclerenchyma. The leaf-gaps are short and the numerous leaf-traces to each leaf depart from the gap margins. The centre of the stem is occupied by hyaline soft tissue and has a diameter of about 1.5 cm. Within this tissue, especially towards the periphery several isolated brown patches of hard tissue are found. No medullary bundles are present.

The peripheral tissue is composed of two layers of cells, the outer being parenchymatous, while the inner one consists of sclerenchyma (fig. 68). The outer margin of the parenchymatous zone, which is about 4-8 cells deep and contains a few irregularly distributed mucilage sacs. There is a transition between the cells of the first and second layer. Sometimes there is so much thickening in the walls of the outer zone due to deposition of additional material that it

becomes impossible in a transverse section to distinguish the cells of this layer from those of the next zone. However, the distinction becomes evident in a longitudinal section.

The second layer is about 36-40 cells deep. The largest fibre observed in this layer measured about 1.5 mm in length and 35 u in breadth, while its wall including the secondary thickening was 7 u thick. Islets of parenchyma are found irregularly distributed within this zone. These parenchymatous masses contain one to several mucilage sacs, and are surrounded by a layer of cubical cells with the characteristic inclusions (fig. 70). The second layer, unlike the first layer ends abruptly and is delimited by a layer of cubical cells (fig. 68). The next layer is composed of parenchymatous cells with intercellular spaces. Numerous mucilage sacs, usually isolated, occur in this layer. Often, departing leaf-traces, which appear reniform in transverse section, are seen in pairs in the protective or in the third layer. The fourth layer of the stem constitutes the outer protective sheath of the meristele, and is composed of sclerenchyma fibres. On either side, this layer is delimited by a layer of cubical cells. The next layer is parenchymatous and has intercellular spaces (fig. 69). This layer is almost uniform in thickness and contains mucilage sacs. The cells of the third and fifth layer contain numerous starch grains.

The meristeles are surrounded by endodermis and the pericycle. The cells of the endodermis show Casparian strips and have thickening on both inner and outer tangential walls. The pericycle, which is 2-4 cells deep, is parenchymatous and often contains reserve food material. As in Cyathea, the meristeles are amphicribral bundles, having the xylem surrounded by phloem. The latter consists of elongated

sieve cells and few parenchyma elements. The sieve cells, which have almost transverse end walls have sieve areas on all walls. Distinction between proto and metaphloem is not possible, but adjacent to the pericycle, several layers of tangential cells are present (fig. 69). The conjunctive parenchyma is usually one to two cells in thickness, but sometimes a sieve cell lies directly next to a tracheid. The xylem consists of scalariform tracheids and xylem parenchyma, and no annular and spiral tracheids are found. A scalariform tracheid has a length of about 2.5 mm and a breadth of 80 u, while its wall including the secondary thickening measures about 10 u.

The pith is parenchymatous and has intercellular spaces. Mucilage sacs, comparatively few in number, are also found in the pith. As in the cyatheas, the inner vascular sheath is differentiated near to the periphery of the medulla and follows the corrugations of the stele. Patches of sclerenchyma, surrounded by cubical cells are found especially towards the periphery of the pith,

THE FROND

Usually more than 35 rhomboidal to oblong-deltoid fronds, which are tripinnate, are found in a very close spiral at the top of the plant. The young fronds show circinate vernation and remain covered by dense hairs. The stipe is chestnut brown in colour, and measures about 90 cm in length. The rachis, which is deep brown towards the base and gradually becomes light brown towards the apex, measures about 60 cm. The sterile segments are toothed. The texture of the frond is rigidly leathery and the veins are free. Both the adaxial and abaxial sides of the lamina are green.

Fig. 72,a

Fig. 72,b

Fig. 72,c

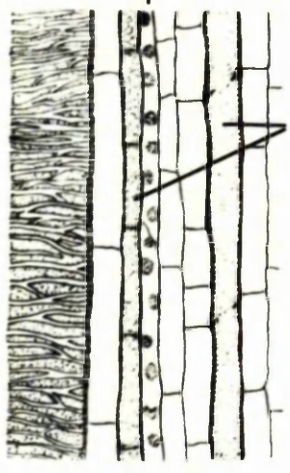


Fig. 73

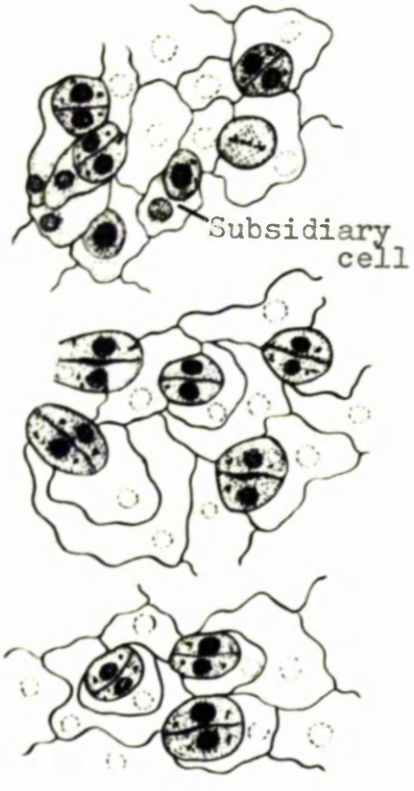


Fig. 74,a

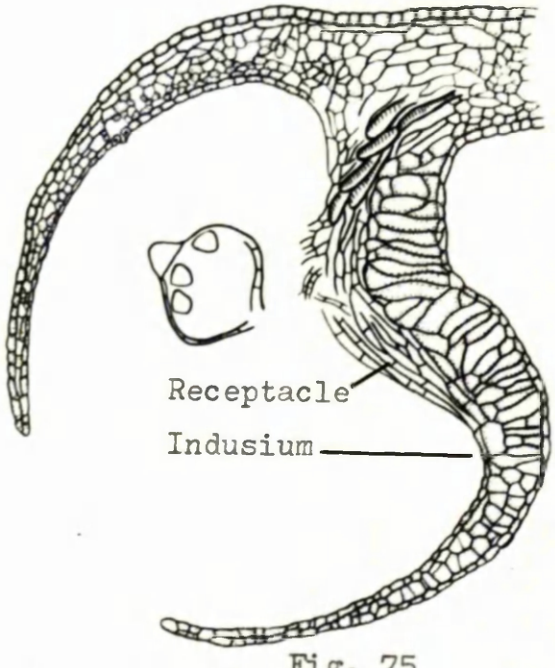


Fig. 75

Fig. 74,b

Fig. 72. Dicksonia squarrosa Sw. Transverse sections of a leaf-axis at different levels (a, extreme base; b, middle of the rachis; c, top of the rachis). Fig. 73. D. squarrosa. L.S. of a part of a petiole. Fig. 74. D. squarrosa.a, Stages in the development of stomata; b, mature stomata. Fig. 75. D. antarctica. V.S. through the receptacle.
(72, x 2.5; 73, x 85; 74,a, x 300; 74,b, x 160; 75, x 100.)

Anatomy

In cross section near the base, the stipe appears circular in outline with a small ridge on the adaxial side. The peripheral tissue is hard, and it encloses the parenchyma in which leaf-traces numbering about 20-25, are found embedded. These traces, as in Cyathea, show a ⅀ 7 shaped arrangement. The individual traces are more or less reniform, and occasionally two neighbouring traces unite laterally to form a W shaped structure (fig. 72,a). Each of the leaf-traces is surrounded by sclerenchyma. A transverse section at about the middle of the rachis shows that all the leaf-traces unite laterally to form a single corrugated strand, which has only the inner protective sheath (fig. 72,b). Another section near the tip of the rachis shows that the wavy structure has lost the inner protective sheath as well (fig. 72,c).

In surface view the epidermal cells of the petiole are rectangular in outline. The outer wall is heavily cutinised and the stomata are absent. On two sides of the petiole, the epidermal continuity is broken by the pneumathodes. The epidermis bears uniseriate, unbranched hairs, which resemble those of the stem. The hypodermis is sclerenchymatous and is about 15 or more cells deep. Sections through the pneumathodes show that the hypodermal sclerenchyma is replaced by highly ventilated, loosely arranged cells without any woolly lignified outgrowths, and covered by the epidermis with stomata. Numerous mucilage sacs are found within the cells of the fundamental tissue of the petiole. These sacs usually occur singly, but if aggregated in groups, their common walls remain intact; frequently, however, near the basal region of the petiole, their end walls break down to form a continuous duct that ends blindly.

The petiolar bundles are surrounded by the endodermis and pericycle. The endodermal cells show characteristic

thickening on their radial walls, but in addition to this, there is a suberin lamella covering the whole inner tangential walls. In young fronds the endodermal cells show tanniniferous contents. The pericycle is 1-4 cells deep and is thin walled. Inside the pericycle is a layer of protophloem cells, which are elongated and narrow. Next to the protophloem there is either a layer of phloem parenchyma or a layer of mucilage cells, which may lie next to the metaphloem or separated from the latter by a layer of parenchyma, one or more cells deep. The sieve cells of the metaphloem are arranged end to end and have their end walls oblique (fig. 73). The sieve areas are found on all walls. Conjunctive parenchyma may be present between the xylem and phloem, or occasionally a sieve tube may lie in direct contact with a scalariform tracheid. Rarely a mucilage cell is found in association with the conjunctive parenchyma. The xylem in transverse section is either V- or W-shaped structure according to the shape of the leaf-trace. Near the angles of V- or W-shaped xylem, there are a few broken annular and spiral tracheids, which constitute the protoxylem. The crushed protoxylem lies directly against the cavity parenchyma, which is composed of loosely arranged parenchymatous cells.

In surface view the epidermal cells of the adaxial side of the lamina appear as rectangular cells with wavy walls; there are no stomata. The cells of this layer are heavily cutinised on their exposed surface. The epidermal cells on the abaxial side are sinuous, and numerous stomata, which are oval in outline are present (fig.74,b). The stomata usually have their long-axes lying parallel to the veins, but their orientation is somewhat variable. The mesophyll cells are spongy throughout.

Development of stomata

The development of stomata was studied in surface view (fig. 74,a). A protoderm cell usually divides anticlinally into two cells by an elliptical or half-elliptical wall. One of the daughter cells may function as the stoma mother-cell, or rarely, before behaving as such, may undergo another division similar to the first one. The nucleus of the stoma mother-cell divides into two, and a wall, which usually lies along the long axis of the oval stoma mother-cell is formed. Frequently, however, this wall may lie at right angles to the long axis of the stoma mother-cell. There is usually considerable deposition of cutinised material on this wall and the two guard cells separate to form the pore. Twin stomata are frequently found in this species.

Sporangia and spores

The sporangia, which are borne on a short receptacle in basipetal succession, are about .4-.45 x .23-.26 mm, and are protected by a bi-valved indusium.

The spores are tetrahedral, anisopolar, and a triangular in polar view, with slightly concave sides. The walls are thick, especially at the angles, which are truncate. The trilete mark is thin and the rays almost reach the equator. The exine is verrucate, and is 2-4 u in thickness. Mature spores are about 50 u across.

Dicksonia antarctica Labill.

YOUNG PLANT

The material used was supplied from the Botanical Garden, Glasgow.

(a) Anatomy of stem

A transverse section of the stem, which in the material investigated was about 1.5 cm in diameter, and a little over 4 cm in length, shows that the anatomical details of this species are almost the same as those of Dicksonia squarrosa. In short, almost all the epidermal cells develop multicellular, unbranched hairs. These hairs unlike those of Dicksonia squarrosa do not show any equisetoid appearance at the transverse septa.

The hypodermal parenchymatous cells, though thick-walled, are easily differentiated from the next fibrous layer. The latter is not limited internally by a layer of cubical cells. The third parenchymatous layer contains mucilage sacs, either isolated or in groups of up to 15. The fourth sclerenchymatous layer is lined on either side by a layer of cubical cells. The degree of maturation of cubical cells is relatively slow as compared with that of the neighbouring tissue. The innermost layer of the cortex is parenchymatous, and does not show any mucilage sacs near the basal part of the stem. They, however, appear near the apex of the stem.

The basal part of the stem is decayed, and the internal structure is not intact. In the region where the internal structure is preserved the stem is solenostelic. Even a few mm above the apparent base, the stele is very much corrugated, and is bounded by an external and an internal endodermis, the cells of which contain tanniniferous bodies and show Casparian

strips. The pericycle is one to two cells deep, but at certain regions, the tangential cells lie directly over the endodermis. It seems certain that young pericyclic cells, under certain conditions, may develop into tangential cells. The phloem is not differentiated into proto and metaphloem.

The xylem as usual is composed of scalariform tracheids and xylem parenchyma, with which every tracheidal element comes in contact at some point or other of its surface. It has been suggested by Williams (1925) that this close association is due to certain physiological reasons.

The method of leaf-trace departure has been described by Williams (1925): it is very similar to that of Cibotium barometz, the chief difference being that the leaf-trace breaks up in the peripheral region before it is cut off from the axial strand.

(b) Anatomy of the petiole

The structure of the petiole is very similar to that of Dicksonia squarrosa. The openings of the pneumathodes on the lateral sides of the petiole are covered by epidermis with stomata and the elements of the ventilating aerenchyma or crumpled sclerenchyma do not show any lignified peg-like out-growths as in Cyathea orientalis.

(c) Anatomy of the lamina

The lamina in transverse section shows a thick cuticle on both upper and lower surfaces. The adaxial epidermal cells are larger than those on the abaxial surface, where the stomata, each surrounded by an epidermal cell, occur. The development of stomata is very similar to that of Dicksonia squarrosa. The mesophyll cells of the adaxial half of the lamina are most compact and angular, whereas those on the abaxial side are oval and loosely arranged.

(d) Anatomy of the root

The epidermis is single layered and some of its cells grow out to form unicellular root hairs. The cortex is differentiated into two regions: the outer zone consists of thin-walled parenchyma, whereas the inner zone consists of thick-walled sclerenchyma, forming a firm mechanical sheath around the central vascular cylinder. The endodermis is single layered: the outer tangential walls of the endodermal cells are lignified, whereas the inner tangential walls are thin; Casparian strips are found on their radial walls. The pericycle is double layered, and consists of thin-walled cells. The xylem is diarch and exarch: each xylem group consists of two protoxylem and two metaxylem elements, and the two groups are united with each other by 6-7 undifferentiated, large, thin-walled cells. Alternating with the xylem groups are arranged the phloem masses.

ADULT PLANT

The sporangia and the spores

The receptacle, which is marginal in position, is flat and extends on to the adaxial surface of the lower indusium (fig. 75). The sporangia are more or less oval and have stalks about 190 u long and 30 u in width. The latter consist of 3-5 rows of cells, 6-8 cells in height, and do not interrupt the oblique annulus. The upper and lower lips of the indusium are not structurally identical. The upper one is very similar to the lamina proper, but the lower one consists of much more elongated and angular cells with small air-spaces. A few stomata occur on the abaxial surface of the lower lip.

The spores are anisopolar, triangular with sides almost

straight and angles broadly rounded. The trilete mark is thin and does not extend up to the equator. The exine is smooth, hyaline, and is less than 1 u thick at the sides, but at least 2 u at the angles. Mature spores are about 52 u across.

Summary

1. The stems are arborescent, and are thickly protected by multicellular, unbranched hairs.

2. As in Cyathea, the stems are dictyostelic, but without any medullary bundles. The stele is very much corrugated, and is protected by sclerotic sheaths.

3. Cubical cells are present both in the cortex and in the pith.

4. Tangential cells are associated with the phloem, and they do not contain any mucilaginous substances.

5. Mucilage cells are present both in the stem and petiole.

6. The leaf-traces are numerous, and as in Cyathea, they show in transverse section the characteristic 7 - shaped arrangement.

7. The sori are marginal in position, but the receptacle shows a tendency to slide on to the adaxial surface of the lower lip of the bivalvate indusium.

8. The structure of the two lips of the indusium is dissimilar: the upper one resembles the lamina but the lower one is different from it.

9. The sporangia have an oblique annulus, and the latter is not interrupted by the stalk. The receptacle is flat.

10. The spores, which are tetrahedral and show trilete mark, have exine usually broadening at the angles.

11. The wall separating the stoma mother-cell from its sister cell, which surrounds the stoma at maturity, may be elliptical as in Cyathea, or half-elliptical. Twin stomata are often found in some species.

Culcita Presl. (1836).

Introduction

The stems are prostrate, but may be ascending. They are, however, never arborescent. The young parts of the stem are protected by stiff and coarse hairs. The fronds are usually deltoid, and the fertile and the sterile pinnae are almost similar. The pinnae are usually borne obliquely on their respective axes, and the costae of the ultimate pinnules are grooved on their upper surface. The sorus is marginal in position and is borne on a vein. The receptacle is raised and flat, and is protected by a bi-valvate indusium. The upper valve is similar to the lamina proper, but the lower one is very different from it. The sporangia, which develop basipetally on the receptacle have an oblique annulus and may or may not be slightly interrupted by the stalk. The spores are tetrahedral.

There are nine species in tropical and subtropical regions, one in the Atlantic Islands and south Spain (Christensen, 1938).

Culcita macrocarpa Presl.

Culcita macrocarpa is a native of Madeira and Azores, and is so abundant there that the woolly covering of the plant was once an article of commerce.

The material for the present study was obtained from the teaching collection of the Department; a few slides were also available from the Gwynne-Vaughan collection.

Culcita macrocarpa Presl.

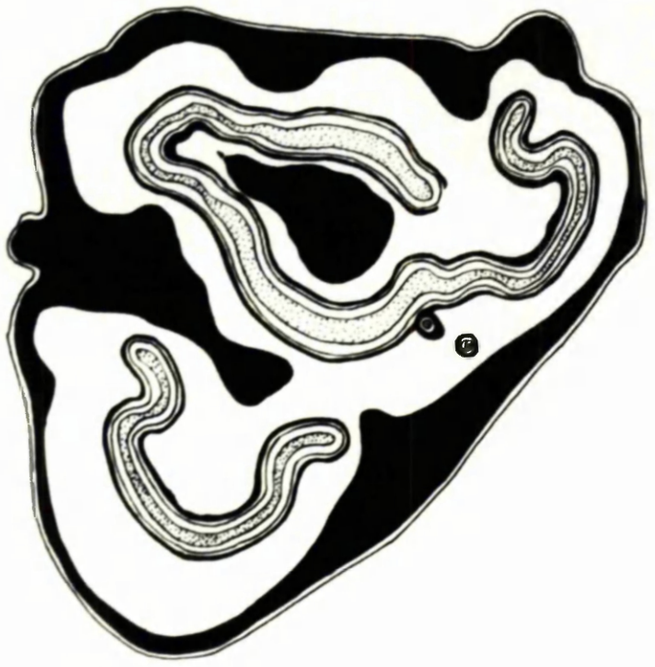
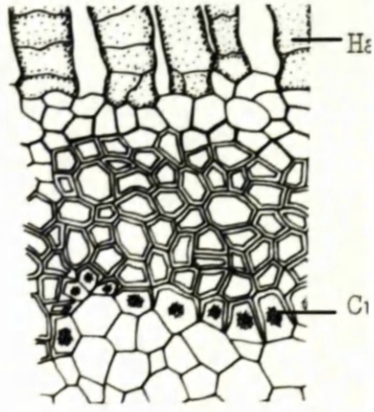


Fig. 76



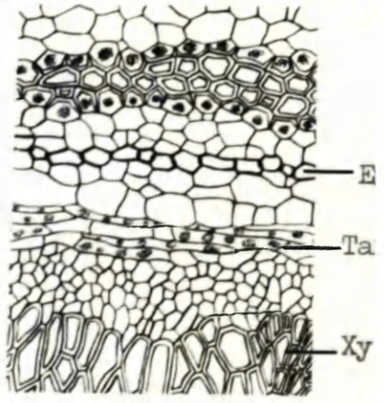


Fig. 77

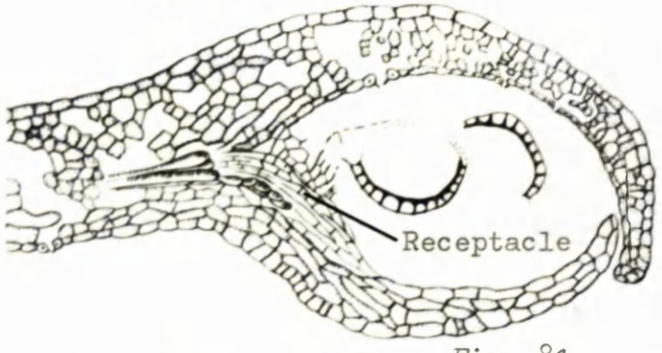
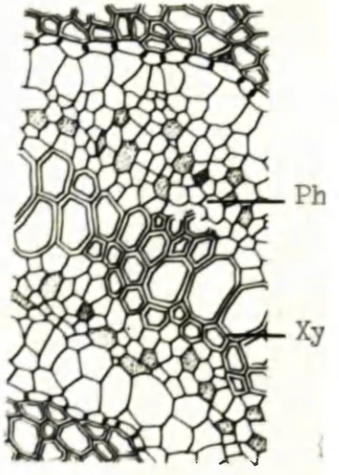


Fig. 81



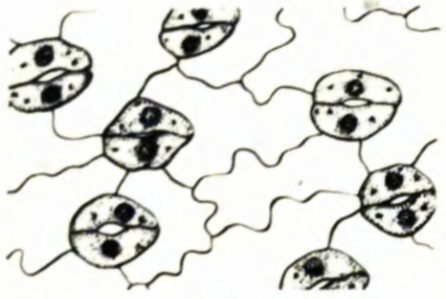


Fig. 80

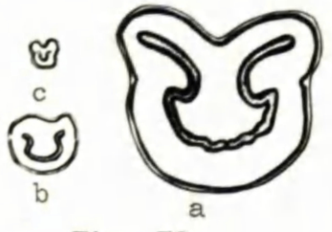


Fig. 79

Fig. 78

Fig. 76. T.S. of stem. Fig. 77. T.S. of stem. Fig. 78. T.S. through a pa
of a petiolar bundle. Fig. 79,a-c. Transverse sections of the frond axis
at different levels (a, near the base; b, middle of the rachis; c, top o
the rachis. Fig. 80. Mature stomata. Fig. 81. Vertical section of the
receptacle. (76, x 8; 77, x 108; 78, x 250; 79, x 3; 80, x 160; 81, x 1

THE STEM

The stem is covered with dense, shining, ferruginous hairs. It develops leaves and adventitious roots on all sides.

Anatomy

In transverse section the stem shows an irregular outline, due to attachment of two to three petiolar bases (fig 76). The latter are comparatively large and often attain the same diameter as the stem. For example, at one region, the stem examined was 0.9 cm across, while one of its petiolar bases measured about 0.85 cm in diameter.

As in the tree ferns, the protective tissue of the stem consists of two layers of cells. The outer, which is limited externally by the epidermis, is 1-5 cells in thickness, and consists of thick-walled parenchymatous elements. Most of the cells of the epidermis bear uniseriate stiff hairs. These are unbranched, and have their cross walls slightly fringed (fig. 77). Next to the hypodermis is the fibrous layer, also of variable thickness. The largest fibre observed in this region measured about 0.3 mm by 20 u, while its wall was about 5 u thick. The transition between these two layers, as usual, is gradual. However, the protective tissue ends abruptly and is limited by a layer of cubical cells, which show the characteristic inclusions. During early stages of development, the cells of this layer show much greater power of division than the neighbouring cells. All the divisions are anticlinal, so that the layer of cubical cells never becomes more than one cell in thickness. The inclusion within the individual cells attains a considerable size even when the nucleus is very active and there is an appreciable thickening of the cell walls. The third layer of the stem consists of thin walled

cells with numerous starch grains. Next to this layer, lies the outer protective sheath of the vascular tissue. The sheath is limited on either side by a layer of cubical cells. The fibres of this zone are longer but more slender than those of the outer sheath of the stem. The largest fibre of this zone measured 0.5 mm by 18 u, and its wall was 4.5 u thick.

The central cylinder is amphiphloic solenostelic, and is circular in outline as seen in a transverse section. The leaf-traces depart as undivided U-shaped strands. The endodermis is of secondary type. The pericycle is 2-4 cells deep. The tangential cells, which may attain 0.2 mm in length and 17.5 u in breadth, are 2-4 cells deep. The distinction between the proto and metaphloem is not possible. The xylem is similar to that of Dicksonia squarrosa, but differs from the latter in having fewer xylem parenchyma cells. The medulla consists of 4 layers: the outer is parenchymatous and is similar to the innermost cortical layer; the second layer is sclerenchymatous and serves as the inner protective tissue of the vascular ring, and is identical with the outer one. The centrally placed sclerenchymatous mass is separated from the inner protective sheath by a layer of parenchymatous cells, containing starch grains, and is surrounded by a layer of cubical cells.

THE FRONDS

The quadripinnate fronds are sub-coriaceous in texture and are arranged in several rows. The rachises are almost glabrous and are deep to medium brown in colour. The lower pinnules are deltoid, and their divisions are ovate. The pneumathodes form an almost continuous line on either side of the rachis and the petiole.

Anatomy

In transverse section the base of the petiole is almost circular with an indentation on the adaxial side (fig. 79,a). As in Cyathea, the peripheral protective layer surrounds the fundamental tissue, but the leaf-trace is not dissected into several bundles to form separate adaxial and abaxial groups. Nevertheless, the leaf-trace resembles the united leaf-traces of the cyatheoid and dicksonioid radises. Though there is no indication of segmentation of the petiolar strand, the abaxial arc is clearly corrugated. The vascular strand as usual is surrounded by a brown protective tissue. Serial sections from the base to the tip of the leaf-axis show that the petiolar strand remains unchanged throughout the entire length of the axis (figs.79,b,c).

The detailed histology of part of the petiolar trace is shown in fig. 78. The openings of the pneumathodes at the sides of the petiole are guarded by stomata, with guard cells usually smaller than those of the epidermis. The hypodermal thin-walled cells of the pneumathodes may be variously branched, and the innermost sclerenchymatous cells are smooth walled.

The lamina

The upper epidermal cells of the lamina are rectangular and wavy. The cells of the abaxial epidermis are more sinuous. The stomata have usually a subsidiary cell adjoining not more than 3/4 of the entire circumference of the stomatal complex (fig.80); but sometimes no subsidiary cell can be recognised. The mesophyll cells are little differentiated.

The receptacle

A section through the receptacle shows that it is flat and that at its base it is supplied with vascular tissue (fig. 81). The sporangia, which are pear-shaped, and are

about 0.3 by .02 mm, develop more or less basipetally and have long stalks, about .04 mm. Sometimes this basipetal succession is not distinct; but certainly there is no evidence of a mixed condition of sporangia. The annulus is vertical, and sometimes is very slightly interrupted by the pedicel. The adaxial lip of the indusium is not different from the lamina proper, but the lower one consists of compactly arranged cells, and does not show any stomata or air spaces.

The spores are tetrahedral, triangular in polar view, anisopolar, trilete, and have rays almost reaching the equator. The angles are broadly rounded, and the sides are straight to strongly concave (fig.103A). The exine is uniformly thickened throughout, hyaline, smooth to faintly granulate, and is about 1 u thick. The mature spores are about 41 u across.

THE ROOT

The roots are slender and much branched. They arise at the base of each leaf close to its junction with the stem.

Anatomy

In older roots the epidermis is replaced by the outermost cortical layers. The outer cortex is sclerenchymatous, while the inner one is thin-walled. The xylem is diarch, and is not in the form of a plate. The two xylem groups are separated from each other by a few large, undifferentiated, thin-walled cells.

Culcita dubei

Transverse section of the petiole

It is structurally similar to that of Culcita macrocarpa. The only difference is that the leaf-trace shows a shape instead of the arrangement of the latter species.

The spores

The spores are tetrahedral, triangular in polar view and have very rounded angles. The trilete mark is prominent and the rays reach the spore equator. The sides of the spore are almost straight and the exine is verrucate, hyaline and about 2 u thick. Mature spores measure about 43 u across.

Summary

1. The plants are prostrate and are covered with hairs.

2. The stem is solenostelic and the vascular tissue is protected by outer and inner sclerotic tissue.

3. Cubical cells and tangential cells are present in the stem.

4. Mucilage cells are absent in the stem but are present in the petiole.

5. The leaf-trace is undivided and may form or structure.

6. The stoma has usually a single subsidiary cell; but sometimes no subsidiary cell can be recognised.

7. The receptacle is flat and is protected by a bivalved indusium. The upper valve of the indusium is very similar in structure to the lamina but the lower one is modified.

8. The spores are triangular in polar view, and have broadly rounded angles.

Thyrsopteris Kunze. (1834)

Introduction

A tree fern, protected with hairs, but without scales. The fronds are deltoid and dimorphic as to their parts. They are quadripinnate, and the pinnae are borne obliquely on their axes. The costae of the ultimate segments are grooved on their upper surface. The sori are marginal, and terminal on veins; each is protected by a cup-shaped indusium.

Thyrsopteris elegans Kunze.

Thyrsopteris elegans, which is the sole species of the genus, is endemic to Juan Fernandez. This is a tree fern with an upright axis, which spreads by means of runners. These latter develop erect shoots at some distance from the parent plant.

The material for the present investigation was obtained from the preserved collection of Prof. F.O. Bower. A few fronds were also available from a plant growing in the Glasgow Botanic Garden.

THE STEM

The erect stem attains a height of about 1 - 1.5 m, and is protected by dense golden hairs and bristles, but without scales.

Anatomy

A transverse section of the stem shows a superficial epidermis, a broad cortex, and the stele, the structure of which varies according to the age of the plant. The single layered epidermis is composed of brown cells covered with a

Thyrsopteris elegans Kunze.

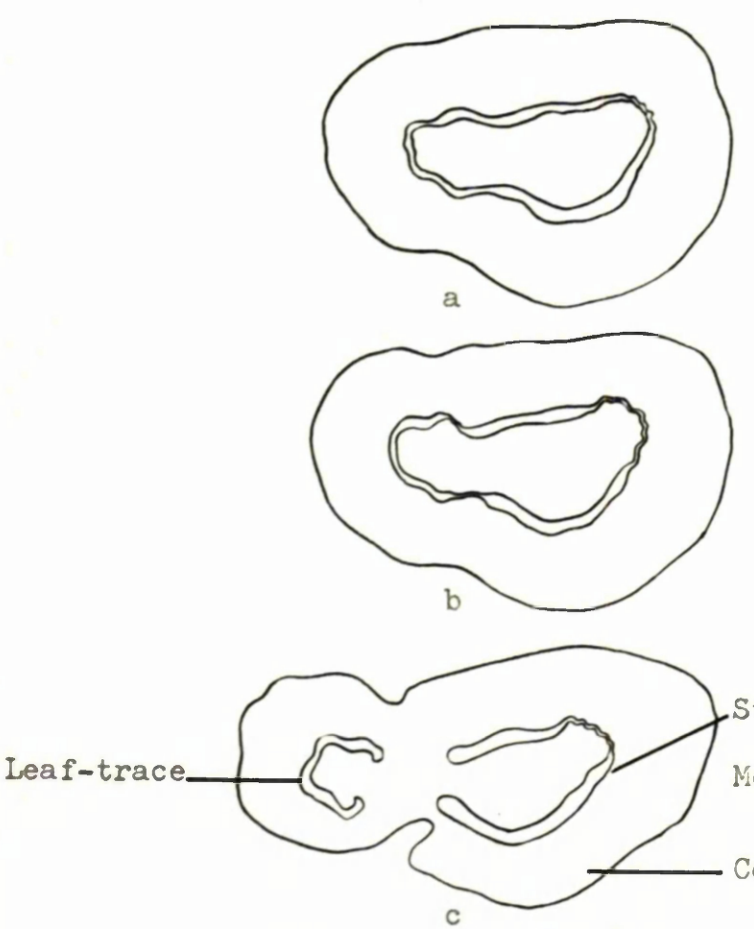


Fig. 82

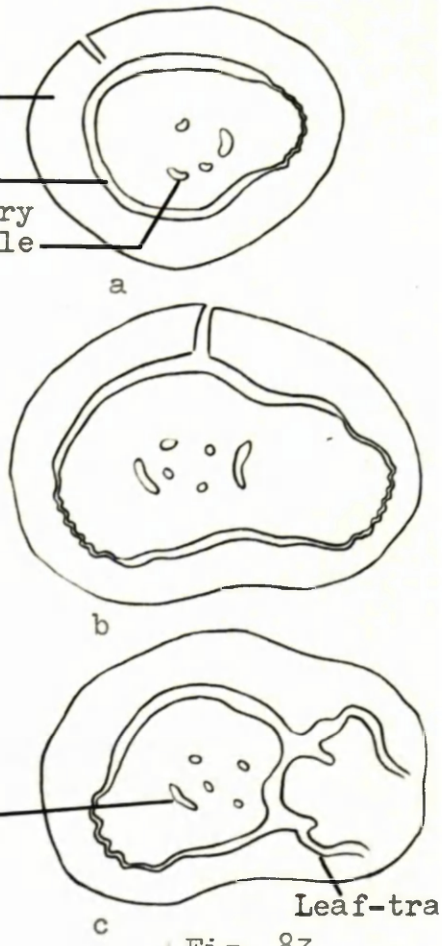


Fig. 83

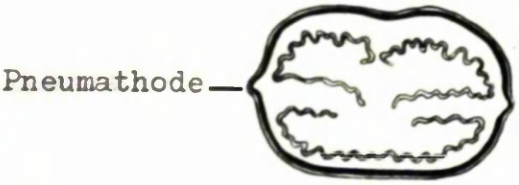


Fig. 84

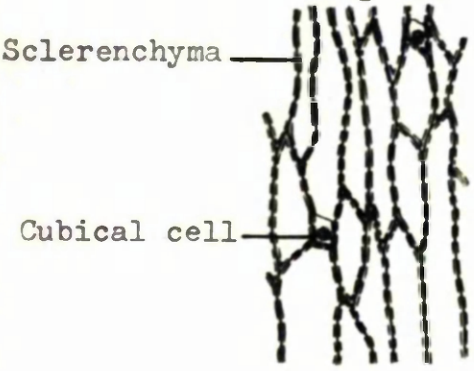


Fig. 85

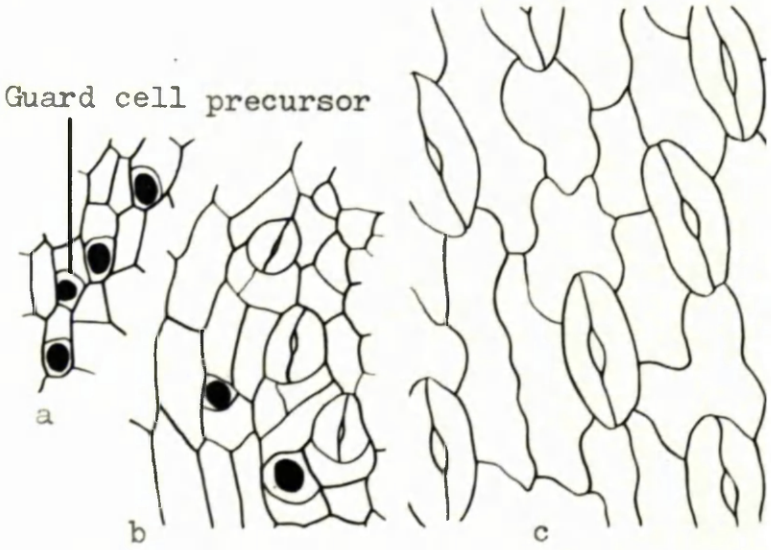


Fig. 86

Fig. 82,a-c. Transverse sections of the stem at different levels showing the departure of a leaf-trace from a basal node. Fig. 83,a-c. Transverse section of a stem at different levels showing the departure of a leaf-trace from a higher node: no leaf-gap is formed due to the compensating action of a medullary bundle. Fig. 84. T.S. of a petiole. Fig. 85. L.S. through a part of th stem cortex. Fig. 86,a-c. Stages in the development of stomata.
(82, x 5; 83, x 2.5; 84, x 2; 85, x 100; 86, x 200.)

thick cuticle. The unbranched epidermal hairs are composed of thin-walled cells and their septa do not show any equisetoid appearance. The hairs towards the growing region may contain mucilage. The bristles are deep brown in colour and may be unicellular or multicellular. They are unbranched and very stiff due to heavy deposition of lignin on their walls. Sometimes their lumen is virtually obliterated. Numerous pits are found on all walls. Frequently, due to periclinal divisions, the bristles become more than one cell in thickness.

The cortex consists of three concentric regions: the outer is variable in thickness and is made up of thick-walled parenchymatous cells. These cells show a gradual transition to the middle sclerenchymatous zone which is unusually thick. The fibres of this zone measure about 450 - 470 by 50 - 65 u and are provided with numerous irregularly scattered simple pits. Numerous cubical cells with their characteristic inclusions are distributed throughout the sclerenchyma in an irregular manner (fig. 85). Usually they are solitary, but sometimes they are found in groups of two, when they have their common wall thin and other walls thick. Very rarely all the walls of a cubical cell may be thickened. The middle cortical zone passes abruptly into the inner, thin-walled parenchymatous layer. Sometimes a few cubical cells may be found between the second and the third cortical layer, but these cells, unlike those of Cyathea or Dicksonia, are not arranged in a continuous layer.

In the young plant, the vascular tissue is a solenostele, but in the mature one, it consists of a peripheral unbroken vascular cylinder with 3 - 6 medullary bundles.

The peripheral vascular ring is constructed according to

the normal fern-type and is amphiphloic. It is externally and internally limited by an endodermal layer. The endodermal cells are slightly elongated tangentially, and prominent Casparian strips are found on their radial walls. Both the inner and the outer pericycle layers are 2 - 3 cells deep, and are parenchymatous. Between the pericycle and the phloem lies a layer of tangential cells, 3 - 4 cells deep. The phloem cannot be differentiated into proto- and metaphloem. The sieve tubes are about 300 by 23 u, and have sieve areas on all walls. The xylem consists mainly of scalariform tracheids intermingled with a few parenchymatous cells. The tracheids of the older stems show a tendency towards irregular pitting on the lateral walls, the pits being small, circular or elliptical in outline. No spiral or annular tracheids are found in the adult stem, so that the position of the protoxylem cannot be ascertained. However, in young plants, the xylem is mesarch.

The pith occupies the greater part of the stem, and can be divided into three regions. The outermost layer is structurally identical with the innermost layer of the cortex, but slightly narrower and ends abruptly. The second layer is sclerenchymatous. Between the first and the second layer, a few cubical cells occur and, like the cortical ones, they are not arranged in a continuous layer. Often they are found irregularly scattered within the second layer, which passes gradually into the inner parenchymatous zone, in which the medullary bundles are embedded. In the older part of the stem, the entire inner part of the medulla, except the cells adjacent to the bundles, becomes sclerenchymatous.

The medullary bundles are of different shapes and sizes, some of them oval, others elongated in transverse section. They are hadrocentric bundles and each of them is surrounded by an individual endodermis. Separated from the endodermis

by a layer of pericycle 1 - 2 cells deep, is a layer of phloem. The solid core of xylem consists mainly of scalariform tracheids though rarely a spiral element is present towards the centre. Tangential cells are absent in the medullary bundles.

The solid construction of the stele

By comparison of successive transverse sections of the stem, the solid construction of the stele was studied. In the young plant, the stele is a cylindrical tube with fusiform perforations, i.e. the leaf-gaps, which do not overlap one another at any level. The leaf-traces pass out as undivided, corrugated straps of the vascular cylinder (figs. 82, a-c). In the mature plant, however, the cylindrical tube contains 3 - 6 irregularly distributed solid strands in the centre. Here the leaf-traces depart in the same way from the peripheral cylinder, but without forming a gap, because medullary bundles function as compensation strands (figs. 82, a-c).

THE FRONDS

The fronds are deltoid, quadripinnate, and are borne in a close spiral. The petiole is purple brown, and is covered with golden hairs and dark brown bristles, which gradually become few in number towards the rachis. There is a furrow on the dorsal side of the petiole and this extends to the entire length of the rachis. Pneumathodes occur on the sides of the petiole, but never form a continuous line. The primary, secondary and the tertiary segments of the fronds are always borne alternately on their respective axes, forming an acute angle towards the acroscopic sides. In these angles, made by the frond segments and their axes, there is always a dark brown tissue. The lowest pinnules are usually largest or equal in size to those of the succeeding ones. The pinnules are also deltoid, and the first segments of the

secondary pinnae are always on the acroscopic side. The incised pinnules are leathery and lanceolate. The lamina is apparently glabrous on both the sides, and the veins are usually unbranched and free. The fertile fronds differ from the sterile ones in being partly dimorphous. The upper pinnae of the fertile fronds are sterile and they resemble the pinnae of the sterile fronds, whereas the lower pinnae are reduced into axes, which bear terminal sori and form a panicle.

Anatomy

In transverse section the petiole is more or less oval with two lateral projections and an adaxial depression (fig. 84). The single layered epidermis is heavily cutinised on its outer surface, and is continuous except at the pneumathodes. The pneumathodes are structurally similar to those of Dicksonia. The hypodermis is sclerenchymatous and is variable in thickness. The fundamental tissue contains no mucilage cells. The vascular trace at the base of the petiole assumes the characteristic 7 shape, but at higher levels, it divides to form two adaxial bundles and an abaxially U-shaped bundle. A discontinuous sclerenchymatous band may line the inner side of the vascular trace. In a transverse section, the tracheids of the leaf-trace are uniseriately arranged, although occasionally they may be more than one cell deep. Cavity parenchyma is prominent and the number of the protoxylem points is variable at different levels of the same frond. The structure of the phloem is similar to that of other dicksonioid ferns. The mucilage cells, which are found in close association with the sieve cells of Dicksonia, could not be detected in this species. A longitudinal section passing through the acroscopic angles, made by primary and secondary pinnae and their axes, shows that

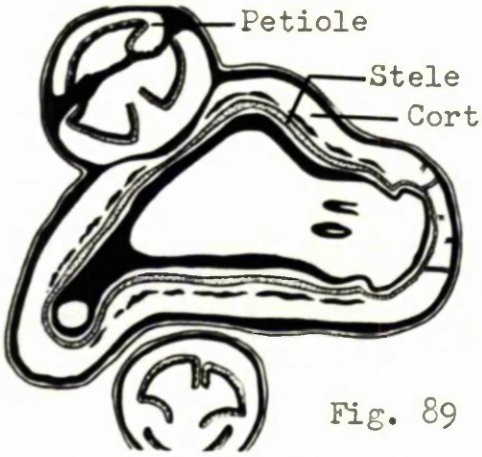


Fig. 89

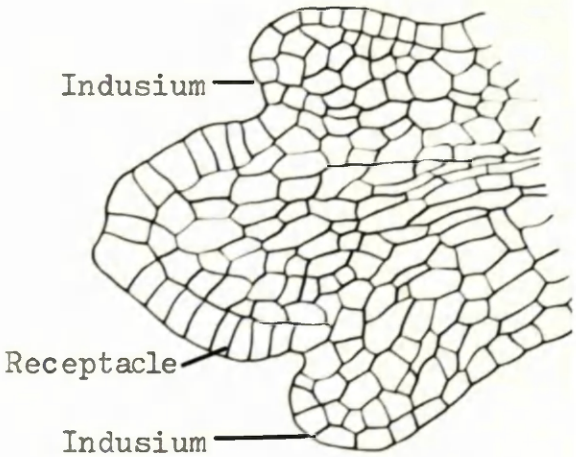


Fig. 87

Fig. 90

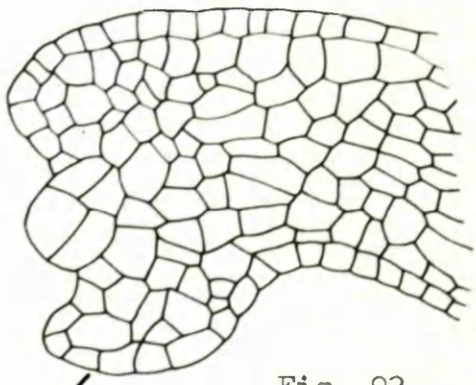


Fig. 92

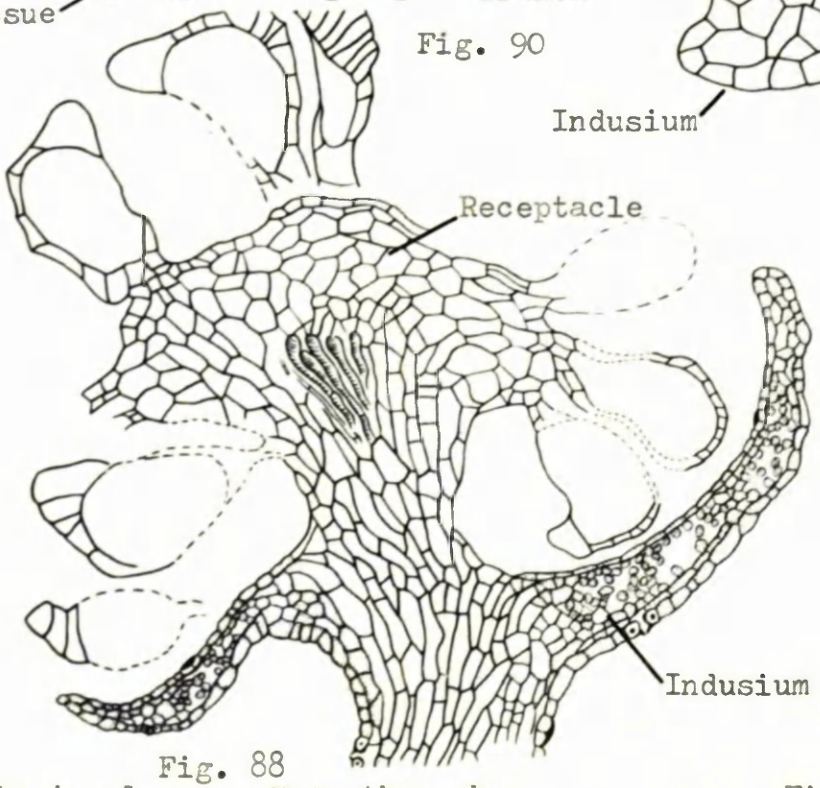


Fig. 88

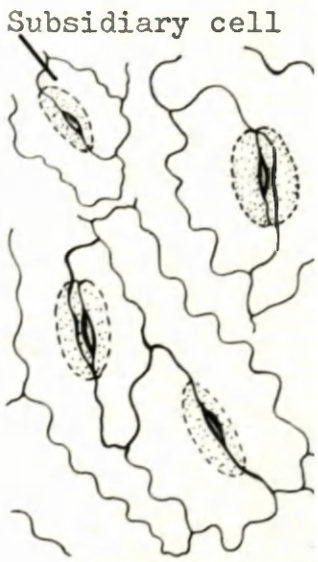


Fig. 91

Fig. 87. Thyrsopteris elegans. V.S. through a young sorus. Fig. 88. T. elegans. V.S. through a mature sorus. Fig. 89. Lophosoria pruinata. T.S. of a stem. Fig. 90. L. pruinata. L.S. of a stem. Fig. 91. L. pruinata. Stomata. Fig. 92. Cibotium schiedei. V.S. of a very young sorus.
(87, x 237; 88, x 114; 89, 90, x .5; 91, x 170; 92, x 235.)

the dark tissue is composed of elongated and pointed fibres. Due to heavy deposition of additional lignin on their walls, these fibres greatly increase the mechanical efficiency of the bases of the primary and secondary pinnae.

A transverse section of the lamina shows that the epidermal cells of the adaxial surface are somewhat larger in size than those of the abaxial one. The stomata are present only on the abaxial side and during the early stages of development they resemble those of Cyathea (figs. 86, a and b). The only striking differences are that the wall separating the guard-cell mother-cell and its sister cell is slightly curved, and in some cases almost straight; also the sister cell of the guard-cell mother-cell undergoes one or more divisions. As a result of these divisions, no subsidiary cells are recognisable (fig. 86, c). This type of stoma may be compared with the anomocytic or irregular celled type of stoma of the dicotyledons (Esau, 1960).

In transverse section a fertile pinnule is more or less circular. The single layered epidermis bears stomata on both sides. The mesophyll consists of spongy parenchyma and shows no differentiation. The vascular trace is concentric.

The development of the receptacle

A longitudinal section of a very young circinately coiled fertile pinnule shows a receptacle developing by the activity of an apical cell (fig. 87). Simultaneously with the development of the receptacle there is a projection of the tissue from both the adaxial and abaxial surfaces. These extensions become the indusium, which during the early stages is slightly two-lipped, but later on sub-globose, and finally a broad cup. A section through such a structure shows that both the abaxial and adaxial part of the cup are structurally similar (fig. 88). The cells of the upper epidermis are elongated and larger than those at the inner side of the cup.

Stomata are present on both the sides. The intervening cells consist of oval to globose spongy parenchyma, recalling the structure of a lamina. However, there is no vascular supply in the indusium.

The receptacle at early stages is conical in section, but later on it becomes circular to oval, and is provided with a comparatively stout and short stalk. The vascular tissue ends blindly in the centre of the receptacle.

The sporangia and the spores

The sporangia, which vary from 170 - 350 by 130 - 180 u, develop basipetally and have very short stalks. The annulus is oblique, and unequally thickened. The dehiscence is lateral.

The spores are tetrahedral, triangular in polar view, anisopolar, and have sides straight to concave. The angles are broadly rounded, and the trilete rays almost reach the equator. The exine, which is hyaline and smooth, is uniformly thickened being about 3 u. The mature spores are about 55 u across.

THE ROOTS

The roots are adventitious in origin in a mature plant, and they develop directly from the peripheral vascular ring of the axis. Some of them pass almost horizontally through the cortex, while others take a downward course for a short distance before finally emerging. A transverse section of the root shows a single layered epidermis of large cells, from which root hairs arise. The cortex consists of an outer sclerenchymatous zone and an inner parenchymatous layer. The endodermis is very distinct. The pericycle is thin-walled and is one cell deep. The stele is diarch and exarch. The phloem forms two bands on either side of the xylem plate.

Summary

1. The plants are dendroid, and are covered with hairs and bristles.

2. The stem is solenostelic, but at later stages develops medullary bundles.

3. Cubical cells are irregularly distributed in the cortex and in the pith.

4. Tangential cells are present in the stem, but mucilage cells are conspicuously absent.

5. The leaf-trace is at first single but later divides into one abaxial and two adaxial bundles. They form the characteristic 7 shape.

6. The wall separating the guard-cell mother-cell and its sister cell is straight or slightly curved; the sister cell undergoes one or more divisions.

7. The receptacle is club-shaped and is protected by a cup-like indusium. Both the upper and lower sides of the cup are structurally identical.

8. The sporangia develop basipetally, and have an oblique annulus. The spores are tetrahedral, and like those of Cyathea and Dicksonia do not showaperispore.

Lophosoria Presl. (1848)

Introduction

The rhizome is hairy, and produces very large fronds, which are usually tripinnate. The sori develop on the lowest acropetal veinlet of the pinna segments. The receptacle is round and exindusiate, while the annulus is oblique and uninterrupted by the pedicel. Lophosoria is a monotypic genus and its sole species, Lophosoria pruinata (Sw.) Presl., is widely distributed in the western Tropics.

Lophosoria pruinata (Sw.) Presl.

The material investigated was collected in Jamaica by Dr. Adams. In all the plants seen by Dr. Adams in their natural habitat, the trunk was horizontal, with the crown always less than one foot from the ground and the petioles ascending vertically. The largest specimen seen was over two foot long, and did not show the habit of an erect stem which had fallen, but rather that of one in which the normal position was horizontal.

THE STEM

Like the majority of the tree ferns, the stem is covered with persistent petiolar bases. Numerous adventitious roots, which develop from all sides of the stem, intermingle and form a thick coating along with the dermal hairs. The stem examined was 9 cms in diameter excluding the outer covering, which was about 3 cms thick. Usually a bud arises on the main stem just below the base of the petiole, but not all petioles are associated with buds. These buds and the tip of the main stem are well protected by brown hairs. Boter (1926

found that the dormant buds at the base of the trunk may develop into runners.

Anatomy

The internal structure of the stem is relatively simple (fig. 89). The epidermis, one cell thick, is composed of elongated cells with slightly thickened external walls. Hairs are the only epidermal appendages. They are multicellular, thin walled and brown in colour. Usually their tips are attenuated, but some are glandular. The cortex is differentiated into three zones: the outer is about 2-3 cells in thickness and consists of vertically elongated parenchymatous cells, which in the older stems are heavily lignified, and are then barely distinguishable from the middle sclerenchymatous layer in a transverse section. The parenchymatous cells are packed with starch grains. The fibres of the middle zone are broad and their walls are greatly thickened and show slit-like pits. Towards the centre, the fibrous zone gradually merges into the inner parenchymatous zone composed of thin-walled cells with intercellular spaces. These cells also contain starch grains. Mucilage cells are absent. The inner cortex contains a discontinuous band of sclerenchyma, the individual strands of which are variable in length and about 2-10 cells deep. At the margins of these strands, solitary cubical cells are found. Sometimes the cubical cells undergo modification and become elongated, but they always contain the characteristic inclusions. There is little variation in the structure of the vascular tissue in a plant at different regions, and also in plants of various ages. The stele is always an amphiphloic solenostele. The stele is demarcated externally from the cortex, and internally from the pith by the clearly recognisable outer and inner endodermis respectively. The walls of the endodermal cells

are brown in colour and they show characteristic thickening on their radial walls. The parenchymatous pericycle is about 2-3 cells deep, and is separated from the phloem by a layer of tangential cells 2-3 cells in thickness. The phloem cannot be differentiated into proto and metaphloem. The xylem consists of scalariform tracheids and parenchyma. The tracheids often show elongated to oval pits. Very rarely in a young plant isolated spiral elements are present, intermingled with the scalariform tracheids. This mesarch development of the xylem, however, cannot be recognised in an adult plant nor in most of the younger plants.

The pith, as in other tree ferns, is differentiated into three zones: both the narrow outer and the broad inner ones are parenchymatous, while the intervening zone consists of sclerenchyma. Isolated cubical cells with the characteristic inclusions are found where the parenchyma and the sclerenchyma meet. These cells are never in a definite row, but they are more frequent in the pith than in the cortex.

Leaf-gaps

The leaf-gaps are fusiform, and are about 3 cms in length and 1.2 cms in breadth. Even in a mature trunk, they do not overlap. A leaf-trace departs as a simple strip and soon becomes corrugated and assumes the characteristic 7 shape.

In those cases where the petioles are associated with the abaxial buds, the solenostelic vascular supply of the bud is connected to the abaxial side of the basal region of the leaf-trace (fig. 90).

The root traces are developed from all sides of the stem and sometimes also from the base of the leaf-traces.

THE FRONDS

The fronds are bi- to tripinnate and are spirally arranged. They are sub-deltoid and often attain a size of about 3 by 1.2 m. Their petioles are dark brown and densely hairy at the bases, while apparently polished towards the apices. There is a continuous line of pneumathodes on either side of the petioles. The rachises are medium brown, and are almost glabrous below, but appressed hairy above. The primary pinnae, about 44 by 18 cms, are ovate-lanceolate, and are alternately arranged. The secondary pinnae are also alternate and are oblong-acuminate, while the ultimate pinnules are lanceolate. They are deeply serrate and their tips are acute. The leathery lamina has its margin slightly incurved and is glaucous beneath. The free veins as well as the costae and the costules are quite hairy.

The anatomy

A transverse section of the petiole shows the epidermis with rectangular cells, about 20 u in length, 12.5 u in each of the other dimensions. The outer wall is considerably thickened. The persistent basal cells of the hairs are numerous and have a diameter of about 50 u. The fundamental tissue of the petiole consists of outer sclerenchymatous and inner parenchymatous regions. Both the epidermis and the hypodermal sclerenchyma are continuous except at the lateral lines, where stomata are found at the openings of the aerating tissue which is structurally similar to that of other tree ferns.

The single 7 leaf-trace may divide in the petiole to form an abaxial and two adaxial strands, which may again undergo fusion within the rachis. The strand is surrounded by a well-defined endodermis which is separated from the thin walled fundamental tissue by a layer of sclerenchymatous cells,

1-3 cells deep. The tracheids of the leaf-trace are of variable diameter, and are usually arranged in 1-2 rows except in the neighbourhood of the protoxylem groups. The trace is endarch with a variable number of protoxylem groups, which are always accompanied by cavity parenchyma. Phloem is present on both the sides of the xylem. The protophloem, which is situated at the outside of the phloem, is separated from the endodermis by a layer of parenchymatous pericycle, 2-3 cells deep. In young fronds a few mucilage cells are found associated with the phloem.

The lamina in transverse section shows a thick cuticle on both the abaxial and adaxial surfaces. The epidermal cells on the abaxial surface are more sinuous than those on the adaxial side. Stomata occur only on the abaxial side, but hairs are present on both surfaces. There is no development of palisade tissue, the bulk of the leaf being composed of loosely arranged mesophyll cells containing chloroplasts. The vascular strands are circular in outline, and are embedded in the mesophyll. Each strand is surrounded by an endodermal layer, and is usually concentric in construction.

The stomata both developmentally and at maturity differ from those of Cyathea. A protoderm cell divides into two by a half-elliptical wall. The larger cell becomes the subsidiary cell and lies parallel to the long axis of the stomatal complex, while the smaller cell divides into the two guard cells. The stomata are sunken (fig. 91).

The sporangia and the spores

The sporangia are borne abaxially on the basal anadromic veinlet of the ultimate pinnules. They develop almost simultaneously in groups of 5-20, more frequently 5-10, on the slightly raised receptacles and are intermingled with hairs. They are almost spherical in shape and have short stalks

composed of 6-8 rows of cells. The annulus is oblique, and the dehiscence is lateral. The spores are tetrahedral, and have a peculiar smooth exine with numerous pits. At one side, the exine extends out to form a rim. The size of the spores varies from 75-80 u.

THE ROOTS

In an adult plant all the roots are adventitious, and are freely branched. Some of them are subterranean, while the majority of them are aerial.

The anatomy

A transverse section of the root shows that the outer walls of the epidermal cells are thickened and suberized, especially in the older regions. The comparatively broad cortex is differentiated into two concentric zones of variable width. The outer cortex is 3-8 cells in width and is composed of angular cells without intercellular spaces. These cells may contain mycorrhizal fungus. The inner cortex, which varies from 4-9 cells in width, is made up of sclerenchymatous fibres with greatly thickened walls. The stele is separated from the cortex by a layer of endodermis with characteristic casparian strips. The stele is diarch and its xylem is usually in the form of a plate with a small group of protoxylem at each end of the plate. The phloem is separated from the endodermis by a two layered pericycle and is present on either side of the xylem plate.

SUMMARY

1. The stem is protected by hairs; adventitious buds arise on the main stem just below base of the petioles.

2. The stem is amphiphloic solenostelic; cubical cells are present; but they are isolated.

3. The single leaf-trace divides in the petiole to form an abaxial and two adaxial strands.

4. The stomata are sunken and have a subsidiary cell, which lies parallel to the long axis of the stomatal complex.

5. Sporangia develop simultaneously, and the spores have a peculiar smooth exine with numerous pits.

Cibotium Kaulfuss (1820).

Introduction

Most of the species are arborescent with a crown of leaves at the apex, while others have prostrate massive stems. Both stem and fronds bear unbranched, soft hairs. The fronds are deltoid, tripinnate or nearly so, and the fertile and sterile leaflets are almost similar in size and shape. The sori are marginal and the indusium is two-lipped: both the lips are similar and differ in structure from the lamina. The sporangia are basipetalous, and have an oblique annulus. The spores are tetrahedral and have no perispore.

There are 13 sp. in East Asia, Hawaiian Islands, and Central America (Christensen, 1938).

Cibotium barometz Link.

Cibotium barometz is widely distributed in Assam (India), South China, Malay Peninsula and Islands. The prostrate plant often reaches a considerable size and bears a tuft of large fronds. The rhizome, which is densely clothed with hairs, sometimes develops lateral shoots. The deltoid fronds with sub-coriaceous texture have stipes often attaining 120 cm in length, and may be tripinnate or nearly so. The base of the stipe is dark brown and hairy, whereas its upper part is glabrous and medium brown in colour. The primary pinnae are borne obliquely on the rachis, whereas the pinnae of the second order (or pinnules) may be oblique or almost at right angles to their axes.

The anatomy of the plant has previously been studied by Gwynne-Vaughan (1903), Bower (1926), and Ogura (1927). The

Cibotium barometz Link.

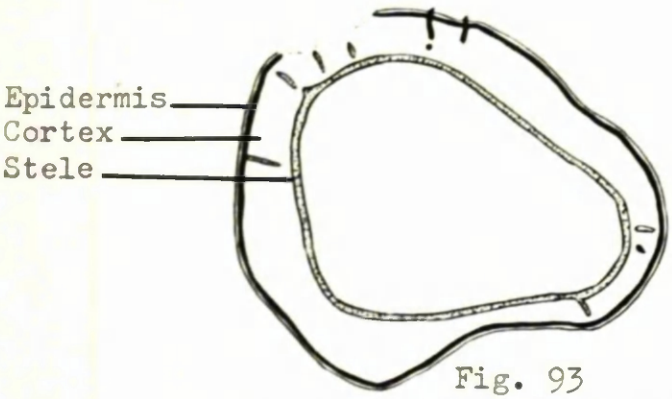


Fig. 93

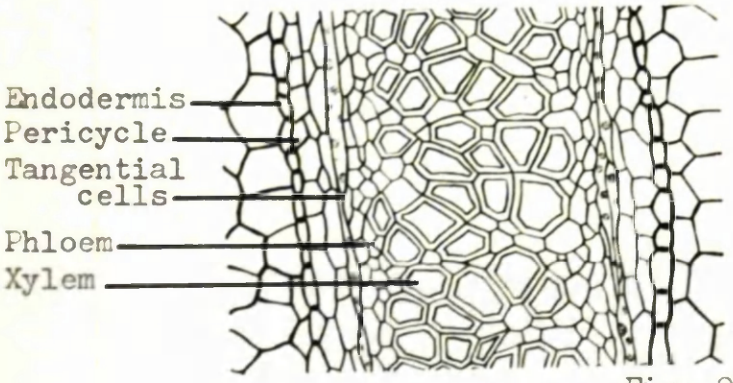


Fig. 94

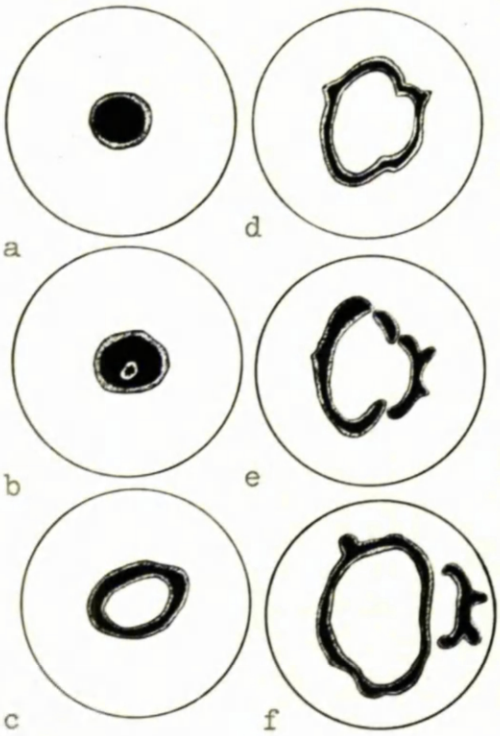


Fig. 95

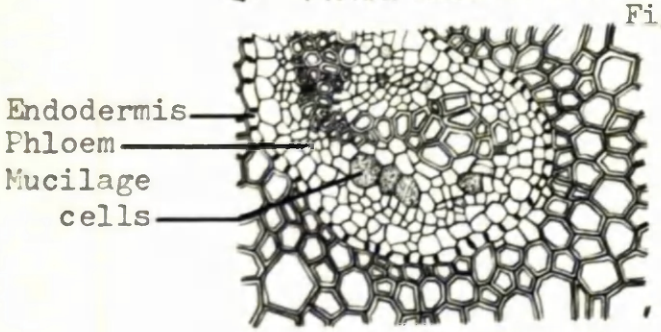


Fig. 97

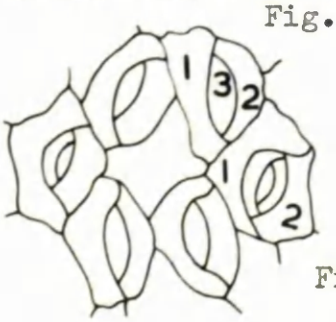


Fig. 98

Fig. 99

Fig. 96

Fig. 93. T.S. of a stem. Fig. 94. T.S. of a part of the vascular ring. Fig. 95. Serial transverse sections of a lateral branch; cortex, only partly shown. Fig. 96. Transverse sections of a leaf-axis at different levels (a, near the base; b, middle of the rachis; c, top of the rachis). Fig. 97. T.S. of a part of a petiolar bundle. Fig. 98. Stages in the development of stomata. Fig. 99. Mature stomata. (93, x 1.5; 94, x 88; 95, x 3; 96, x 5; 97, x 125; 98, x 200; 99, x 150.)

account of it here given is mainly based upon the slides available from the Gwynne-Vaughan collection.

(a) Anatomy of Rhizome

A transverse section of the rhizome (Fig. 93) shows a large solenostele which, unlike the steles of Cyathea and Dicksonia, is not accompanied by sclerotic sheaths. The leaf-traces are undivided at their origin but soon become divided into separate strands. Numerous root-traces are inserted on the main stelar ring and on the proximal regions of the leaf-traces. It may be mentioned here that Ogura (1927) described Japanese specimens as showing a dictyostelic condition.

The epidermis, bearing uniseriate hairs, is heavily cutinised. Below this lies a narrow zone of parenchyma merging into a band of sclerenchyma. Inside the latter there is a broad band of parenchyma without mucilage sacs. No cubical cells are present at the junction of the sclerenchyma and this inner zone of parenchyma.

The detailed structure of the vascular tissue is essentially similar to that of Dicksonia squarrosa. The endodermis is secondary in type; tangential cells are present inside the pericycle.

The pith is entirely parenchymatous; no mucilage cells are present.

(b) Anatomy of lateral shoots

Serial transverse sections through the lateral shoot show that near the base it is protostelic (fig.95,a); a little further up, in the centre of the stele, there is an appearance of parenchyma mixed with tracheids (fig.95,b). Above this level, it becomes an amphiphloic solenostele from which leaf-traces, like those of the rhizomatous portion, depart, (figs.95c-f). Adventitious roots are also developed

from the undissected leaf-traces of the lateral shoots. Histologically the lateral shoots are identical with the rhizomatous part.

(c) Anatomy of the leaf-axis

Fig. 96 represents the cross sections of the leaf-axis at different levels. Near the base of the petiole, the petiolar bundle undergoes repeated divisions to form three groups of traces. As in Cyathea two of them are adaxial and form structures, whereas the abaxial one forms a semicircle (fig. 96,a). Within the rachis these bundles undergo lateral fusion and form three wavy bundles (fig. 96,b). Towards the tip of rachis, these bundles unite to form a single strongly corrugated bundle (fig.96,c).

In histological detail the petiole is identical with that of Dicksonia squarrosa. Mucilage-sacs, which are absent in the stem, are found associated with the phloem (fig. 97); no mucilage-sacs are, however, found within the fundamental tissue of the petiole. The aerating cells of the pneumathodes do not show any lignified out-growths, and they are covered by an epidermis with stomata.

(d) T.S. of the fertile leaflet

A section through the fertile leaflet shows that the receptacle is raised, only to a slight extent. It is protected by the two-lipped indusium, which unlike the lamina, is composed of compact cells with no air spaces. Stomata are usually absent on both the lips, but very rarely one or more stomata may be found on the abaxial surface of the upper indusial lip.

(e) The stomata

The stomata are very different from those of Cyathea, Dicksonia, and Culcita. A mature stoma is usually surrounded by 3 cells which differ slightly in shape from the ordinary epidermal cells. These subsidiary cells are closely related ontogenetically to the guard cells, and flank the stoma parallel to the long axis of the guard cells(fig. 99). This type of stomata may be compared with the paracytic type or parallel-celled type of stomata of the dicotyledons (Esau, 1960).

An initial cell first divides by an anticlinal wall, into two cells (fig. 98). The larger cell again divides in the same way, but the ends of the separating wall touch the wall of the first cell. In the same way one or more cells may be cut off. The central cell functions as the guard-cell mother-cell and forms two guard cells in the usual manner.

(f) The sporangia and the spores

The sporangia, which are more or less ellipsoidal in form, vary from 350 - 380 x 250 - 275 u. The annulus is incomplete and obliquely vertical, and is not interrupted by the stalk, which is about 250 u long.

The spores are tetrahedral, triangular in polar view, and anisopolar. The angles are narrow, and the sides are straight to concave. The exine is hyaline, faintly verrucate, and is about 2.5 u in thickness. The mature spores are about 68 u across.

(g) Development of indusium

The development of the indusium was studied in Cibotium schiedei. The margin of the young frond at first becomes flattened, and from the centre of it develops the initial cell of the receptacle (fig. 92). By the activity of this cell, and its daughter cells, the flattened receptacle is formed. The two lips of the indusium develop by extension and multiplication of the cells of the upper and lower surfaces of the frond. During the early stages of development these two lips and the lamina are identical in structure. But later, the lamina develops spongy mesophyll cells, and stomata on the abaxial surface. The cells of the two indusial lips, however, remain compact, and no intercellular spaces are usually formed. In surface view the epidermal cells of the indusium are sinuous, and usually stomata are lacking. In very exceptional cases, however, very few stomata appear on the abaxial surface of the upper lip. The lips which are structurally almost identical, and are devoid of any vascular tissue, differ from the lamina proper in colour and texture from a very early stage of development. Very often, unbranched, multicellular hairs are developed on the adaxial surface of the lower lip.

On the receptacle the sporangia are developed in basipetal succession.

Cibotium hawaiense Nakai and Ogura.

(a) The stem

The stem is erect and is covered with numerous persistent leaf-bases and adventitious roots. The leaf-bases never fall off leaving scars on the stem, a feature so characteristic of Cyathea.

The protective tissue of the stem is composed of two layers of cells, the outer is parenchymatous, and is about 1.5 mm thick, while the inner one, which is about 2 mm thick, is composed of short fibres. The fundamental tissue consists of thin-walled cells filled with starch grains, and does not show any mucilage cells and cubical cells. No other mechanical tissue, except that at the periphery, is found in the stem.

The vascular tissue is dictyostelic, and its detailed histology is essentially similar to that of Cibotium barometz.

The majority of the hairs protecting the stem are thin-walled, but a few of them are stiff and thick-walled. The latter are narrow and pointed. Both types of hairs are unbranched and dark brown in colour.

(b) The petiole

The internal structure of the petiole agrees with that of C. barometz.

(c) The roots

The transverse section of the root shows that the epidermis has numerous root hairs. The cortex is usually divided into two zones: the outer three to seven layers are usually thin-walled, while the inner cortex consists of lignified cells. The endodermis is single layered. The stele is diarch. The two protoxylem groups are connected by metaxylem tracheids, so that the xylem forms a plate, on either side of which there lies the phloem.

SUMMARY.

1. The stem is solenostelic or dictyostelic.

2. No mechanical tissues excepting those which form the outer protective tissue are found in the stem.

3. No mucilage cells or cubical cells are found in the stem, but tangential cells are present outside the phloem.

4. The leaf-traces, as in Cyathea, form one semicircular inferior series, and two superior series of the characteristic pattern.

5. More than two subsidiary cells flank the stoma parallel with the long axis of the guard cells.

6. The receptacle is marginal and little elongated. The two indusial lips are structurally distinct from the lamina proper.

Metaxya Presl. (1836).

Introduction

Metaxya is a handsome creeping fern with large pinnate fronds, about a meter long, with the tips hanging over. The pinnae are long-lanceolate, and profusely hairy during the early stages of development. They are serrate at the tip, but elsewhere smooth or abnormally lobed. The sporangia are borne abaxially on flat receptacles. The indusium is absent and the spores are tetrahedral.

It is a monotypic genus.

Metaxya rostrata Presl.

Metaxya rostrata is a native of many localities in Tropical America and is also found in Trinidad. The plant has been found in Suriname by Dr. K. U. Kramer (personal communication, 1961) in three different ecological situations. Firstly, it was found in the mature state on a hillock of iron-ore and gravel in a rain forest, and in the young state on a moss covered tree trunk in the vicinity of an open forest. Secondly, both young and mature plants were found growing on banks of sand in the deep shades of a creek on a hill slope, and thirdly, the plant was found in an area of sandstone, which is covered by a savanna forest. In this forest Metaxya was found to be fairly common in damp shaded places on cliffs bordering waterfalls and creeks, accompanied by members of the Hymenophyllaceae, also Lindsaya sp., Cyclodium sp. or Dryopteris meniscioides.

The following anatomical description is based on material kindly furnished by Dr. Kramer in February, 1961.

Metaxya rostrata Presl.

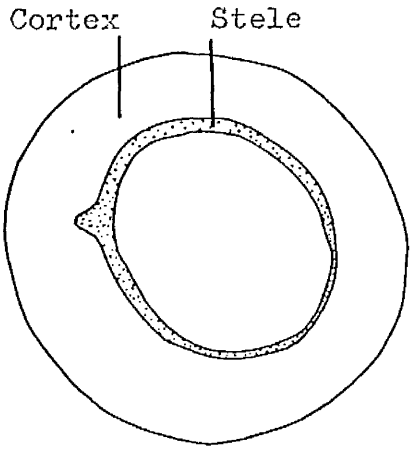


Fig. 100

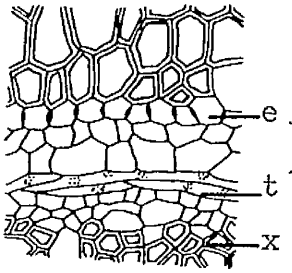


Fig. 101

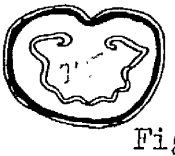


Fig. 102

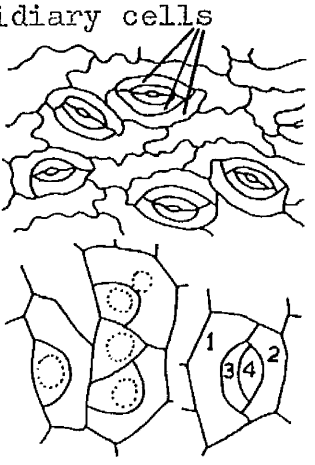


Fig. 103

Fig. 100. T.S. of a stem. Fig. 101. T.S. of a part of the stem showing endodermis (e), tangential cells (t), xylem (x). Fig. 102. T.S. of a petiole. Fig. 103. Stages in the development of stomata.
(100, x 3; 101, x 125; 102, x 2.5; 103, x 90.)

HABIT

The stem is stout and clothed with numerous hard, dark roots and ragged persistent leaf-bases. The branches occur frequently and they are similar to those of Lophosoria; they appear on the abaxial side of the leaf-bases.

STEM ANATOMY

(a) Epidermis and cortex

Most of the cells of the external layer of the stem elongate radially to form hairs, so that the epidermis is hardly recognised as a distinct layer even near the growing region of the stem. The young hairs consist of a single row of elongated cells, each of which usually has delicate walls: the transverse walls are slightly wavy near the margin. The tips of the hairs are broadly attenuated. Unlike the young hairs, the mature hairs are however stiff, with transverse septa thrown into deep and regular corrugations with the result that those hairs show exactly the same 'equisetoid' appearance as those of Dicksonia squarrosa.

The cortex consists of three primary regions. There is an outer cortex of one to three layers of parenchymatous elements. The middle region is occupied by a layer of sclerenchymatous cells. The inner region of the cortex is made up of thin-walled cells and is limited internally by the endodermis. In the older part of the stem, however, the sclerenchymatous zone gradually extends inward until the entire inner part becomes sclerenchymatous.

(b) The stele

The central cylinder in the adult plants is an amphiphloic solenostele (fig. 100). The average diameter of the stele is about 1.2 cm and the thickness of the ring from the external to the internal endodermis is 0.5 - 1 mm. The

endodermis is of secondary type and in the young condition contains tannin. The thin-walled pericycle is about 2-3 cells deep and is followed by a layer of tangential cells, 1-4 cells thick (fig. 101). The xylem, as in the tree ferns, consists of scalariform tracheids and a few parenchymatous cells. The pits of the tracheids are very much elongated, and the tendency to form oval pits is not evident.

The medulla in the young condition consists of parenchymatous elements packed with starch grains, but in the older part of the stem, it sometimes becomes completely sclerenchymatous. No cubical cells or mucilage cells are found in the stem.

(c) The lateral branches

The lateral branches, which are borne on the abaxial side of the petiole are solenostelic from the very beginning. As in Lophosoria, the medulla of these branches is in direct contact with that of the parent plant, and the vascular tissue of these branches is a downward extension of the leaf-trace.

THE FRONDS

The fronds are uni-pinnate and in the young condition are covered with profusely branched hairs. The pinnae are leathery, and are about 29 x 4.5 cm. The tips of each pinna are deeply serrated, but the margins are smooth or rarely dentate. The regular serration of the tip (and occasionally elsewhere), probably suggests that the unipinnate condition of this fern is a derived one, and, probably, each of these pinnae represents a modified pinna of the second order of a cyathean frond. It is interesting to note in this connection that Dr. Kramer found lobed pinnae in some young plants of Metaxya (Holttum, '61, personal communication).

The pinnae are borne obliquely on the rachis forming an acute angle towards the acroscopic side of the frond. The

veins are parallel, and occasionally forked. Sometimes two parallel veins fuse half-way or near the margin: occasionally the branches of a bifurcating vein fuse again to form a single vein.

(a) Anatomy of the petiole

The epidermis of the petiole is interrupted at the pneumathodes. The openings of the pneumathodes are covered by the epidermis with stomata and the cell walls of the ventilating tissue do not show any lignified outgrowths. The ground tissue of a young petiole consists of thin-walled elements, but in the mature one it becomes very hard and sclerotic. The petiolar trace comes off from the stem as a simple meristele, and soon assumes a complicated shape. (fig.102). The leaf-trace even in the mature frond remains undivided throughout. The endodermis of a young petiolar strand contains tannin. Here the tracheids are arranged in 1-4 rows. The protoxylem strands vary greatly in number, depending largely on the size of the bundle. No mucilage sacs are found in the petiole.

(b) Anatomy of the lamina

The epidermal cells are chlorenchymatous. The mesophyll cells are more or less isodiametric, and are not differentiated. However, towards the adaxial half of the lamina there are only a few air spaces.

The stomata are very similar to those of Cibotium (fig. 103). Each stoma is surrounded by three or more subsidiary cells, which lie parallel to the long axis of the guard-cells. All subsidiary cells and the guard-cell mother cell have a common origin.

THE ROOT

Adventitious roots are formed in relation to the leaf-traces and a transverse section of a stem shows numerous root traces extending radially from the base of each leaf-trace and out through the cortex. There are no unusual features in the structure of the root.

THE RECEPTACLE

The development of the receptacle has been studied in the young pinnae, which are circinately coiled. The first evidence of the development of the receptacle is seen as a hump of meristematic tissue on the abaxial side of the frond. There does not seem to be any apical initial responsible for this development. Copious hairs, branched or unbranched, are found all around the receptacle. The receptacle is slightly raised and is semicircular in a transverse section. From the early condition the receptacles are supplied with vascular tissue. Often more than one receptacle develops on a single vein.

THE SPORANGIA AND THE SPORES

The sporangia develop simultaneously as in Lophosoria. The annulus is slightly oblique, and may or may not be slightly interrupted by the pedicel. The mature sporangia vary from 500 - 550 x 220 - 240 u.

The spores are roundly triangular in polar view, and are anisopolar. The trilete mark is prominent, and the suture and the lips are visible. The rays extend up to the equator of the central body, which is surrounded by a thick, more or less smooth girdle, about 4 u wide. Mature spores are 37 - 50 u across.

SUMMARY

1. The stem is protected by unbranched hairs, but the hairs of the fronds may be unbranched or variously branched.

2. The stem is solenostelic. Tangential cells form a layer of 1 - 4 cells deep. Cubical cells and mucilage cells are, however, absent.

3. The petiolar strand comes off as a single meristele. It soon assumes characteristic 7 shape and remains undivided.

4. The stomata are very similar to those of Cibotium.

5. The receptacles develop on the abaxial surface.

6. Suture and lips are visible in the trilete mark of the tetrahedral spores.

SUMMARY AND DISCUSSION

(a) Habit

A comparative survey of the genera described above shows that these plants are diverse in size and habit. The rhizomatous condition is found in Culcita, Metaxya and Cibotium, though in Cibotium, erect stocks are not uncommon. It may be noted, however, that the rhizomes are never dorsiventral, thus differing from those of the Gleicheniaceae. In Lophosoria the stem is arborescent, but at maturity the trunk lies obliquely horizontal. Thyrsopteris is a small tree, while in Cyathea and Dicksonia the plant may be several meters high.

Branching in these genera on the whole is weak: many species do not branch, while others branch only sparsely. As a result of branching, certain species of Cyathea (e.g. C. mexicana, C. aculeata) become more or less shrubby (Bower, 1926). In Lophosoria, Metaxya and Thyrsopteris, though the main stem is usually unbranched, numerous lateral branches are developed and these serve for the vegetative propagation of the plants.

(b) Dermal appendages

The young parts of the stem in the majority of the genera are covered with multicellular hairs, which are morphologically very diverse in the group. These hairs are usually unbranched but in Cyathea they may be variously branched. (It may be noted, however, that in very exceptional cases, certain hairs on the fronds of Cibotium scheidei may show branching.) In Dicksonia and Culcita, as the hairs mature, they become coarse and more or less stiff, whereas in Cibotium they always remain soft. The hairs of Dicksonia squarrosa and Metaxya are peculiar in having an equisetoid appearance due to frilling of the peripheral region of the transverse septa. In

Thyrsopteris and Cyathea pulcherrima stiff bristles, which are more than one cell thick and, in the latter species, have setiform projections, are associated with hairs.

Scales are universally present in Cyathea. The developmental history of these scales indicates their probable evolutionary origin from hairs. The early stages of development of hairs and scales are almost identical. Those initials, which are destined to form hairs, after a few transverse divisions, elongate and divide no further, while in a scale initial the cell divisions are continued further, not only in a transverse direction but also longitudinally, thus giving rise to a flat structure. In structure and development the cyatheoid scales are of two types: the setiferous and the flabelloid. The setiferous scales develop from simple hairs and may therefore be considered as relatively primitive; whereas the flabelloid scales are advanced, as they develop from peltate hairs, which are certainly more advanced than the simple hairs. Some flabelloid scales of Cyathea bear superficial hairs and these are probably the highest form of scale structure in the group. The bristles are also formed by the elaboration of hairs. In many species of Cyathea, and also in Dicksonia squarrosa, the scales or hairs are ultimately shed and their bases are elevated into peg-like structures by the active division of the persisting basal cells. These structures are more conspicuous in Cyathea than in Dicksonia.

(c) Stem structure

In the majority of the genera the stem is protected by persistent leaf-bases, and adventitious roots, as well as the dermal appendages already described. In many species of Cyathea and Dicksonia the leaf-bases leave a scar on the stem after their death and decay. These scars are protected

externally by a hard covering, through which the remnants of leaf-traces project. The number and arrangement of these traces is variable in different species although the fundamental plan is the same in all.

The internal structure of the stem of these ferns is complex. In all genera the tissue below the epidermis consists of two layers of cells. The relative thickness of these layers is variable in different genera and even in different species. The cells of the outer layer, though parenchymatous, are usually thick walled and gradually pass into the next fibrous layer, which not only protects the stem but also gives it mechanical support. In Dicksonia squarrosa a few mucilage sacs, either isolated or in groups of two or more, are present in the outer parenchymatous layer. In all the species examined, except for Dicksonia squarrosa and Thyrsopteris, the fibrous layer is homogeneous in construction, but in the latter (Thyrsopteris) numerous cubical cells with their characteristic inclusions are irregularly distributed throughout the unusually thick layer of sclerenchyma. In Dicksonia squarrosa islets of parenchyma are found irregularly distributed within this zone. The parenchymatous masses contain one to several mucilage sacs and are surrounded by a layer of cubical cells. The second layer, unlike the first, ends abruptly and in Culcita macrocarpa, Dicksonia squarrosa, Cyathea pulcherrima, C. orientalis it is delimited by a layer of cubical cells. The cortical zone inside the external fibrous layer may be entirely parenchymatous, as in Cibotium and Thyrsopteris, or there may be, as in Dicksonia, Culcita, Lophosoria, and Cyathea, a zone of sclerenchyma lying between a broad outer zone and a narrower inner one of parenchyme. In Metaxya, the cortical zone, inside the external fibrous layer, is parenchymatous in the young condition, but in the older parts of the plant the fibrous zone extends inward until

the inner part becomes entirely sclerenchymatous. The inner sclerenchymatous band of Dicksonia, Cyathea, Culcita and Lophosoria acts as the outer protective sheath of the stele, the corrugation of which it follows closely. The sheath is thin in Lophosoria, but thick in Cyathea, where, in transverse section, it may appear as a continuous or a discontinuous layer according to the species. In all the genera where the fibrous layer is present it is limited both externally and internally by a layer of cubical cells.

The stele in all the genera considered shows a wide range of structure. Gwynne-Vaughan (1903), while studying the ontogeny of the sporeling of Cyathea excelsa, found a protostelic condition at the base of the stem. But, except for the lateral branches of Cibotium baromotz, none of the plants investigated, showed a protostelic condition. The very base of the youngest plants available showed a well developed solenostele. The solenostelic condition is permanently retained even in the adult plants of Cibotium, Culcita, Metaxya and Lophosoria as a natural consequence of the distant insertion of the leaves. Thyrsopteris develops a few bundles inside a continuous peripheral vascular cylinder. In Dicksonia and Cyathea, as the young plants grow, the simple solenostele is elaborated into a dictyostelic condition due to overlapping of leaf-gaps. As growth continues, numerous medullary bundles develop in Cyathea either directly from the pith or as inner projections of the meristeles. The meristeles of Dicksonia and Cyathea, especially those of the former, become very much corrugated. However complicated the vascular tissue may be, it is always delimited from the surrounding tissue by an endodermis which is usually of the secondary type. In certain cases, the endodermal cells may contain tanniniferous bodies or some other substances.

The vascular tissue in all genera is constructed after the general fern type in having the central xylem mass surrounded by phloem. The scalariform tracheids of the xylem have irregular pittings, the pits being elongated, oval or almost circular in outline. Even in the very young plants the xylem is never purely tracheidal. Vessels, which are found in certain advanced ferns, are absent in all the species investigated. Except in very rare cases the protoxylem elements cannot be detected. In those cases where the spiral elements can be detected, the xylem is always mesarch.

The phloem is composed of sieve cells and phloem parenchyma. The sieve cells are arranged in vertical series, and in most cases, a distinction between the proto- and meta-phloem is not possible. In all these ferns, either inside the protophloem or immediately outside the phloem layer, there is a layer of tangential cells. The tangential cells are always provided with sieve areas, but vary in their contents. Sometimes, as in the young plants of Cyathea contaminans, they are filled with mucilage-like substances, while in other cases, these are absent. Ogura (1927) found mucilage cells in certain Japanese species of Cyathea outside the phloem layer. He had also recorded the presence of tangential cells in the same region for other Japanese species and it seems certain that he did not appreciate the fact that the tangential cells may contain mucilaginous substances under certain conditions. The pericycle in all cases is parenchymatous and varies from 2-4 cells in thickness.

The medulla shows wide variation. In Cibotium, it occupies a greater part of the stem and is wholly parenchymatous. In Dicksonia, Cyathea, Culcita and Lophosoria it is divided into three regions. The outermost layer is parenchymatous, and in the first two genera contains mucilage cells. The

second layer is sclerenchymatous and acts as the inner sheath of the vascular tissue. The thickness of this layer is almost identical with that of the outer sheath. As in the case of the outer sheath, this layer may or may not be continuous according to the species, and its inner margin lying towards the centre may be smooth or dentate. In all cases, it is delimited from the adjacent parenchyma by a layer of cubical cells. In Metaxya, the medulla in the young condition is parenchymatous, but in the older part of the stem it becomes completely sclerenchymatous. In Thyrsopteris, although the medulla can be divided into three regions in the young state, at maturity the entire inner part of the medulla, except the cells adjacent to the bundles, becomes sclerotic. In Culcita the central part of the medulla is sclerenchymatous. In Cyathea and Thyrsopteris medullary bundles are always present. These bundles in Cyathea may be without any fibrous sheath, but more frequently they are accompanied by sclerenchymatous tissue, which may or may not completely surround them. Surrounding each medullary bundle is an endodermis. The pericycle of the bundles is usually single layered and consists of parenchymatous cells. The bundles are hadrocentric, and sometimes may have parenchymatous tissue in the centre of the xylem. The endarch protoxylem consists of tracheids with helical thickening, whereas the tracheids of the metaxylem are scalariform-pitted. The phloem does not show any tangential cells, and a distinction between the proto- and metaphloem is not evident.

The leaf-gaps in all the cases are fusiform. In Cyathea and Dicksonia the vascular tissue lying at the margins of a leaf-gap bends outward very conspicuously. In Thyrsopteris, due to the compensating action of the medullary bundles, there is no formation of leaf-gaps in the older part of the stem.

(d) Roots

The roots in all the mature plants are adventitious in origin and develop from all sides of the stem. The general structure of the root in these genera does not differ from that usual in the leptosporangiate ferns. The cortex in many species is either partly or almost completely fibrous, but in certain cases, it remains parenchymatous. The endodermis in all genera is well developed and there are no thin walled passage cells, which are sometimes found in certain leptosporangiate ferns. The xylem is diarch and exarch and in certain cases some of the tracheids of the metaxylem remain unlignified.

(e) Fronds

The fronds in all the genera are spirally arranged, though the phyllotaxy varies even in the same individual at different regions. The fronds of Cyathea and Dicksonia are more or less rhomboidal in outline but in Thyrsopteris, Culcita, and Lophosoria they are deltoid. It is possible that the deltoid condition has been derived from the rhomboidal state.

Although the fundamental plan of construction of the pneumathodes in all these genera is the same, they are of two types: in the first type, for example in Cyathea orientalis, the cells of aerating tissue have numerous lignified peg-like projections on their walls, whereas in the other type (which is very common), the walls of the cells of this aerating tissue are smooth and do not have any lignified projections. In certain cases the epidermis of the pneumathodes possesses stomata which may be persistent, or ephemeral. In other cases the first formed pneumathodes are provided with stomata but later formed ones have no stomata and communicate with the exterior by separation of the epidermal cells.

The fundamental tissue of the petiole consists mainly of parenchymatous cells, but often part of it, especially towards

the vascular tissue, becomes sclerenchymatous. In Cyathea and Dicksonia numerous mucilage sacs are found embedded in the fundamental tissue.

The vascular tissue of the petiole in Culcita and Metaxya is a continuous band; in Cibotium, Lophosoria and Thyrsopteris it is at first a continuous band but later divides at a higher level into three traces; in Cyathea and Dicksonia there are numerous traces. Though the number of leaf-traces is variable in these genera, they always form a typical

7-shaped structure. The condition of the leaf-trace in Culcita macrocarpa is and this is undoubtedly derived from that of Culcita dubei. The structure of the petiolar bundle or bundles shows little variation. The endodermal cells of those bundles apart from their characteristic thickening on their radial walls may contain tanniniferous substances. The pericycle consists of 1-4 layers of large parenchymatous cells with thin walls. Inside the pericycle lies a layer of protophloem. In Cyathea, Dicksonia and Cibotium mucilage cells are found inside the protophloem layer. This is unique in the ferns. The metaphloem consists of sieve cells in 3-8 layers and abundant parenchyma. The parenchyma associated with the scalariform-pitted elements of the metaxylem may show tanniniferous substances. The number of the protoxylem groups is variable, and they are always accompanied by cavity parenchyma, which consists of loosely arranged, comparatively large, thin-walled cells. The protoxylem elements show annular or spiral thickening.

The lamina in all genera is fairly coriaceous. The cells of the upper epidermis have sinuous walls, but the walls become more or less straight over the veins. The cells are often chlorenchymatous. Usually the mesophyll is not very clearly differentiated, but those cells towards the lower epidermis are more spongy than those near the adaxial surface.

The stomata are confined to the lower epidermis, and they show a range in structure and development. In Thyrsopteris, the wall separating the guard-cell mother-cell and its sister cell is almost straight or slightly curved, while in Cyathea it is elliptical: in Dicksonia some of them are elliptical, but others are half-elliptical, and in Lophosoria the wall is always half-elliptical. In Metaxya and Cibotium, at least three such half-elliptical walls are formed before the differentiation of the guard-cell mother-cell.

In Cyathea, the stomata at maturity have a single subsidiary cell. This cell encircles the stomaand is adnate with it at one point only. In Dicksonia some of the stomata, like those of Cyathea, have a subsidiary cell encircling the stomatal complex, but here the subsidiary cell never adjoins the guard cells over more than 3/4 of the entire circumference of the stomatal complex. In others, however, like those of Lophosoria, the subsidiary cell flanks the stomata more or less at one side only. Metaxya and Cibotium have at least three subsidiary cells lying parallel to the long axis of the guard-cells, in Thyrsopteris no subsidiary cells can be recognised at maturity and finally, in Culcita some of the stomata have a subsidiary cell adjoining not more than 3/4 of the entire circumference of the stomatal complex; the remainder of the stomata have no recognisable subsidiary cells.

Leaf dimorphism is of universal occurrence in Thyrsopteris and Dicksonia. In the latter, the lamina of the fertile frond is less expanded, whereas in the former, the fertile fronds are dimorphic as to their parts. The lower pinnae of a Thyrsopteris frond are fertile; they are slender and consist of numerous pinnules each with a terminal sorus, whereas the upper pinnae are coriaceous and similar to those of a sterile frond. The leaf dimorphism in those two genera probably represents a primitive condition and is probably due

to complete or partial failure of syngenesis, i.e. the lateral fusion or webbing of sporangia bearing axes, and is different from the condition found in Onoclea or Cryptogramma, where leaf dimorphism is believed to be due to reduction in the lamina of the fertile fronds (Eames, 1936). No such marked dimorphism is however present in other genera.

(f) Receptacle

In the mature condition, the position and shape of the receptacle in these genera are both variable. In Thyrsopteris the receptacle is strictly marginal and is more or less circular in section. In Cyathea it is hemispherical to globose, and is superficial in position. The superficial receptacle of Lophosoria is rounded and flat, whereas in Metaxya it is slightly raised and semicircular in transverse section. In Dicksonia, Culcita and Cibotium the receptacles are distinctly flattened, though not very conspicuously in the latter genus. Developmental study shows that the receptacle in Cibotium and Thyrsopteris originates at the margin. It has already been seen earlier that in the latter the position remains unchanged even at maturity, but in the former there is a tendency of the receptacle to slide down on to the adaxial surface of the lower indusium. In Cyathea dealbata, Bower (1899) has shown that the receptacle originates on the abaxial surface, but in this species, some of the receptacles can certainly be traced to the marginal meristem. (It is significant to note that in Gleichenia, which according to Bower, had acquired the superficial character during the Palaeozoic period, and stands at the bottom of the superficial series, the receptacle does not always originate as a smooth swelling at the abaxial surface as has been stated by Bower (1899). In this fern also, at least some of the receptacles (fig. 66/A) show the 'phyletic slide' similar to those of

Dennstaedtia punctiloba, which was included by Bower in his Dicksoniaceae.) In Metaxya, however, the receptacle originates as a smooth swelling on the abaxial surface. The primitive position for the receptacle is the marginal one; the change of position to the abaxial side of the leaf is obviously a derived condition.

(g) Indusium

The indusia in these genera are outstandingly different. In Thyrsopteris the indusium is obscurely bivalvate when young, but becomes a complete cup at maturity. Structurally the cup is similar on both the abaxial and adaxial sides: the distribution of stomata and intercellular spaces is the same in both. In Dicksonia, Cibotium and Culcita the indusium is two-lipped from the very beginning and this condition is maintained in later stages of development. The adaxial lip of Dicksonia and Culcita is not very different from the lamina proper, but the abaxial one is delicate, whereas in Cibotium both lips are distinct from the substance of the lamina. Anatomically also, the upper lip of Dicksonia is different from the lower one, and has more stomata and intercellular spaces, whereas in Cibotium both lips are similar, are composed of comparatively compact tissue and have very few stomata on them. Although the young stage of the indusium in Cyathea dealbata is comparable to a bi-lipped condition, it is a closed cup at maturity. The thickness of the indusial cup in this species is variable in different indusia of the same frond. It consists of very compactly arranged cells and stomata are absent. The indusium of Cyathea capensis is saucer like, while in Cyathea contaminans, Lophosoria, and Metaxya the indusia are absent.

(h) Morphological nature of the indusium in Cyathea

The morphological nature of the indusium in Cyathea has been the subject of much discussion for a long time. Robert Brown (1810) first of all suggested that the indusium in Hemitelia (= Cyathea) represents an involucre. Hooker (1864) interpreted this as equivalent to the dermal scales found on the vegetative organs. Mettenius (1856) objected to this idea as the indusium, unlike a scale, is persistent, and is different in the manner in which it is borne on the receptacle. Goebel (1918) interpreted the hemitelioid indusium as the derivative of the dicksonioid condition. Bower (1923) agreed with Hooker and considered that the differences between the scale and indusium is due to specialization in the latter. His inference is based on comparative stages illustrated by mature sori of Gleichenia, Lophosoria, Alsophila (=Cyathea), Hemitelia (= Cyathea) and Cyathea. He believed that these ferns form a phyletic series, which acquired the superficial position of sori during a very early geological period, presumably the Palaeozoic. In Gleichenia the sorus is naked, and there are no hairs intermingled with the sporangia; in Lophosoria and Alsophila (= Cyathea) simple hairs are found scattered among the sporangia; sometimes in Alsophila (= Cyathea) and constantly in Hemitelia (= Cyathea) a spathe-like indusium protects the receptacle from one side, while in Cyathea the sporangia are protected by a complete cup. The gradual increase of complexity shown by the indusium of these ferns led Bower to believe that the cup-like indusium in Cyathea was evolved from primitive hairs, presumably as a lateral extension or by webbing or by both.

However, the ontogeny of the indusium of Cyathea dealbata does not support Bower's hypothesis. If we believe that recapitulation during ontogeny is a definite help in solving the real morphological nature of an organ, the cyathean

indusium is certainly a derivative of the dicksonioid type. In the early stages of development, the meristematic leaf-margin of Cyathea dealbata forms more or less a three-lobed structure as seen in section. The middle one develops into the receptacle and, at least in certain cases, it is certainly a continuation of the leaf-margin (fig.65,a), but subsequently it is shifted to the lower side of the adaxial lobe due to rapid growth of the latter. The lower lobe or flap from its inception is a multicellular structure and does not give the impression of having developed from a single initial cell, as is the case with the dermal appendages. During this stage of development the upper and lower lobes can be compared with the two-lipped condition of Cibotium. The upper lip continues its growth as part of the lamina. The lower lip, which at this stage is a mere flap can be interpreted as the extension of the lower margin of the frond. Gradually this flap extends round the receptacle and becomes saucer like and ultimately develops into a closed cup. Thus the developmental history of the indusium in this species shows that it has not developed by lateral extension or by the webbing of several hairs but rather from the lower lip of an indusium such as that of Cibotium. Had the indusium been formed by the lateral extension of a hair, the developmental stages would have shown features comparable to those described for the development of a typical dermal scale.

The developmental stages of the indusium in Cyathea capensis show that it remains flap-like in most cases, but in rare cases the flap-like indusium terminates in a number of hair-like segments. It may be inferred that the indusium in Cyathea is not constant, probably because of the fact that during the phyletic slide of the sorus from the marginal to the superficial condition, the indusial flap has become plastic - in certain cases it forms a cup, in other cases it remains in

its archaic condition, and in still others it becomes vestigial.

(i) The sporangia and the spores

The sporangia in most of the genera are much alike in diagnostic characters. In all except Lophosoria and Metaxya they develop basipetally though sometimes in Culcita macrocarpa the latter formed sporangia may not be clearly basipetalous. In Lophosoria and Metaxya the sporangia develop simultaneously. The sporangial stalk may be short or long according to the species, but in all cases the annulus ib oblique-vertical and is not interrupted by the stalk except in Culcita and sometimes in Metaxya, where there is slight interruption. The dehiscence of the sporangium is transverse to lateral.

The spores in all the species are totrahedral. Their sides are usually straight or concave. The angles may be narrow or rounded. In Dicksonia the walls are thick, especially at the angles, which are truncate. The exine may be smooth, faintly granulate or verrucate. The trilete mark is present in all cases, but it may be distinct or faint. The spores of Lophosoria are very distinct and have a peculiar exine, which at one side, extends out to form a rim (fig.103/A).

(j) Taxonomy

Though these ferns vary a great deal due to diversity in elaboration of certain structural features, they constitute a uniform group as do other fern families. The common characters which unite them in a single group are:
1. Formation of the protective sheath of stem by two layers of cells - outer parenchymatous and inner sclerenchymatous.
2. Presence of cubical cells with characteristic inclusions in the stem (except in Cibotium and Metaxya). 3. Formation of tengential cells in the phloem of the stem. 4. Usual

Spores of Cyatheaceae

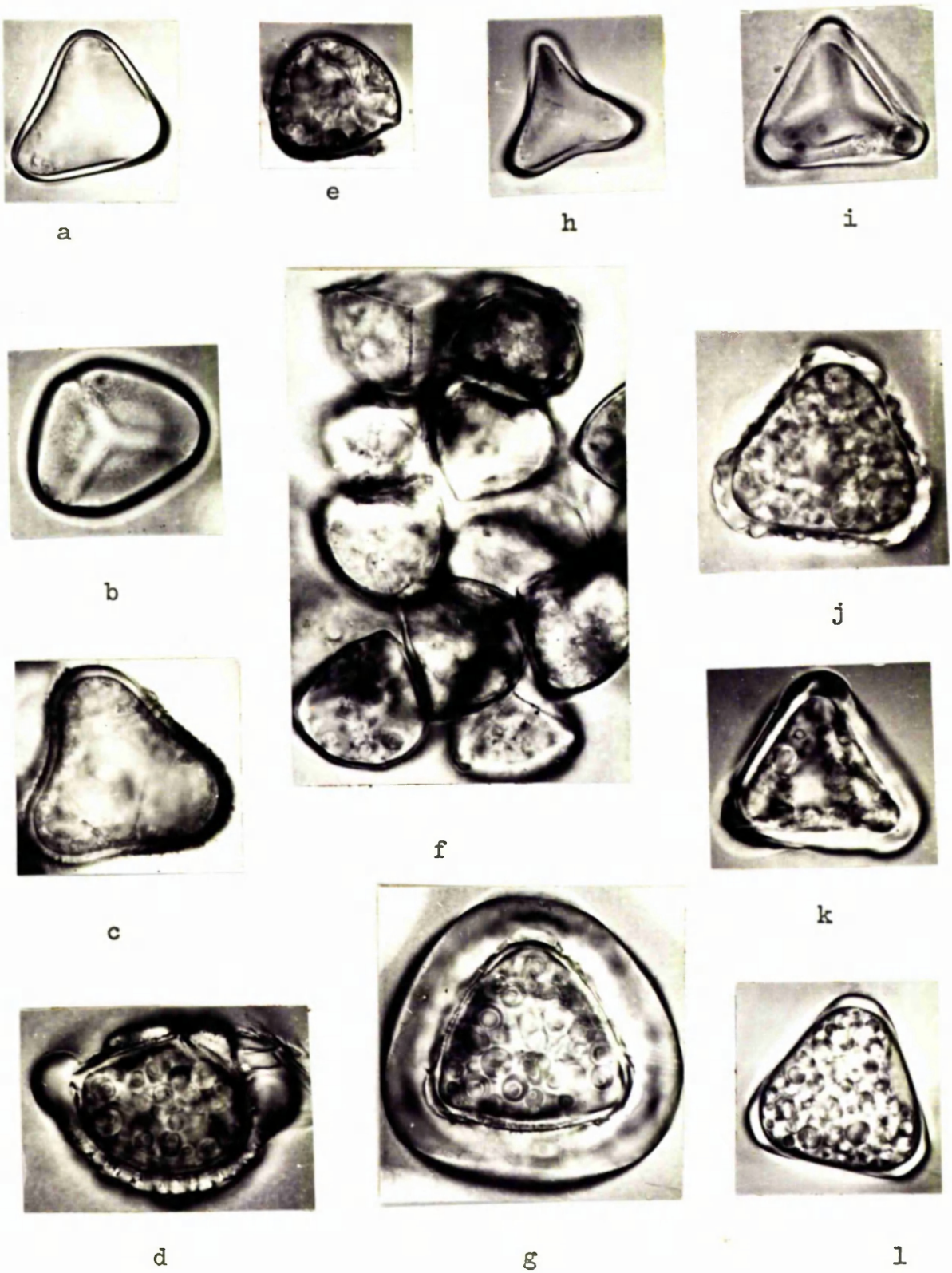


Fig.103/A: a and b, Culcita macrocarpa Presl.; c, Cyathea pulcherrima Copel.; d and g, Lophosoria pruinata (Sw.) Presl.; e, Metaxya rostrata Presl.; f, Cyathea costalisora Copel.; h, C. contaminans (Wall.) Copel.; i, Thyrsopteris elegans Kunze, j, Dicksonia squarrosa Sw.; k, Cibotium barometz Link.; l, Dicksonia antarctica Labill.

(all, x 500.)

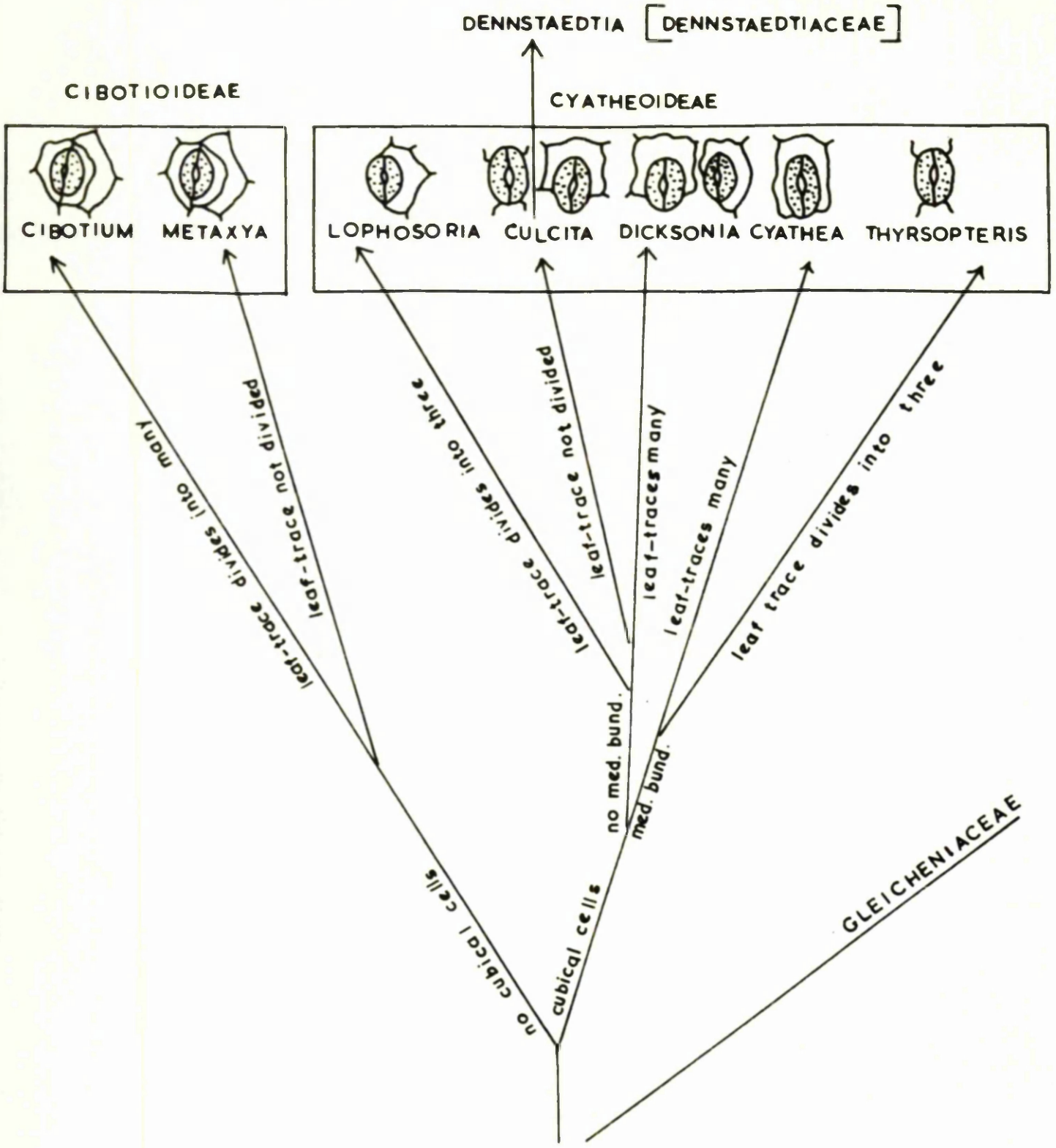


Fig. 103/B. Diagram showing the phylogenetic relationship of the different genera as proposed in this thesis.

absence of annular or spiral tracheids in the mature stem. 5. The characteristic assumption of 7 shape by the petiolar bundle or bundles in spite of the variation in their number. 6. Sporangia with oblique-vertical annulus and usual transverse to lateral dehiscence. 7. Tetrahedral spores without perispore, and 8. In certain cases formation of mucilage cells either in the cortex of the stem or petiole or in the phloem of the latter. All the genera have most of these characters, although some of them are not confined only to this group. For example, Osmunda develops tangential cells and mucilage cells; but no other pteridophytes have this peculiar assemblage of characters. While the combination of these characters keeps all these genera together, the presence of tangential cells and the typical pattern of the leaf-trace or traces are enough to distinguish them from any of the known leptosporangiate ferns. It seems certain that constancy of all these characters in these ferns is due to close phylogenetic connections between them as uniform homoplastic development in so many respects in widely separated ferns is improbable. So the inclusion of all the genera in the Cyatheaceae by Christ (1897), and later by Diels (1902), Christensen (1906) and others, has the merit of being based on structural similarities rather than on opinion. Thus Bower's emphasis on the prevalence of the two major lines of descent in the tree ferns, referred to as the Marginales and the Superficiales, and the subsequent segregation of Dicksonia, and its related genera from Cyathea can no longer be regarded as natural.

Taxonomically it seems reasonable to attach primary importance to the presence or absence of the cubical cells and also to the structure of the stomata, and to place all the genera of the Cyatheaceae into two subfamilies, the Cyathoideae and the Cibotioideae (fig.103/B). The

Cyatheoideae includes five genera and has cubical cells, and stomata each with a subsidiary cell which almost encircles the guard-cells or, in other examples, lies parallel to their long axis. Both types of stomata may be present in the same leaf. In some cases, the subsidiary cell is not recognisable. Cyathea and Thyrsopteris differ from the rest of the sub-family in having medullary bundles. The genus Culcita has always a single leaf-trace; in Lophosoria and Thyrsopteris though the leaf-trace is a single strand at the base, higher up it divides opposite the lateral pneumathodes of the petiole into three straps. Dicksonia and Cyathea, however, have numerous traces. The sub-family Cibotioideae contains but two genera, and has no cubical cells in the stem. The stomata always show at least three subsidiary cells lying parallel to the long axis of the guard-cells. Metaxya has a single undivided leaf-trace, while in Cibotium the leaf-trace divides into many strands.

As regards the division of the genus Cyathea (in the sense used here), it seems natural to divide this genus into two sub-genera on the basis of the scale character as has been proposed by Holttum (1957). It has been seen earlier that not only morphologically but also in developmental detail the scales are different. The setiferous scales, which are characteristic of the sub-genus Sphaeropteris develop from simple hairs, whereas the flabelloid scales, which are present in the sub-genus Gymnosphaera, develop from peltate hairs. In neither sub-genus are both setiferous and flabelloid scales present.

Relationship of Cyatheaceae

The structural resemblance between Cyathea and Gleichenia has been emphasised by Bower (1926), Holttum (1949) and others. The two are undoubtedly much alike in having superficial sori at maturity, setiferous scales and similar leaf-form in the primitive species. The leaf-trace of Gleichenia is C-shaped (inrolled horse shoe) and is not very different from that of Cyathea in its pattern. Despite this similarity these two genera stand apart from each other in several important characters: the rhizome of Gleichenia is dorsiventral, its leaves show false dichotomy and grow in stages. (However, the fronds of very young plants of Gleichenia glauca do complete their growth, and resemble the frond of young plants of Cyathea (Holttum, 1957,b)). The hairs of Gleichenia are stiff, unicellular but branched; the scales though setiferous, are peltate; sporangia dehisce longitudinally. No cubical cells or tangential cells, which are universally present in the Cyathoaceae, are found in the stems of Gleichenia. These data therefore suggest that the Cyathoaceae have not certainly been derived directly from the Gleicheniaceae, but that they have probably evolved from a common stock.

Bower included Dennstaedtia within his Dicksoniaceae. Holttum has shown the relationship of this genus with Culcita. These two genera agree in having a creeping habit, hairs as the dermal appendages, sori marginal in origin, but in the former genus, they slide downwards more conspicuously. The stomata are also very similar (see figs. 254, and 266, Conard, 1908). The more or less U-shaped leaf-strand of Dennstaedtia is not very different from that of Culcita. The presence of cubical cells with the characteristic crystals certainly shows that they are very closely related. However, the absence of

tangential cells justifies its separation from the Cyatheaceae (in the sense here used).

Structural resemblances between the Schizaeaceae and dicksonioid plants have been emphasised. Schizaea does not show any cubical cells or tangential cells. A full discussion of the relationship of Schizaea with the Cyatheaceae is, however, deferred until a detailed histological study of the genus is made.

Onoclea and Dryopteris were thought to have a direct relationship with the Cytheas, but the anatomical details of those genera do not support such a conclusion.

The presence of tangential cells and mucilage cells in the stems of Osmundaceae indicates a possible relationship between these plants and the Cyatheaceae.

PART II

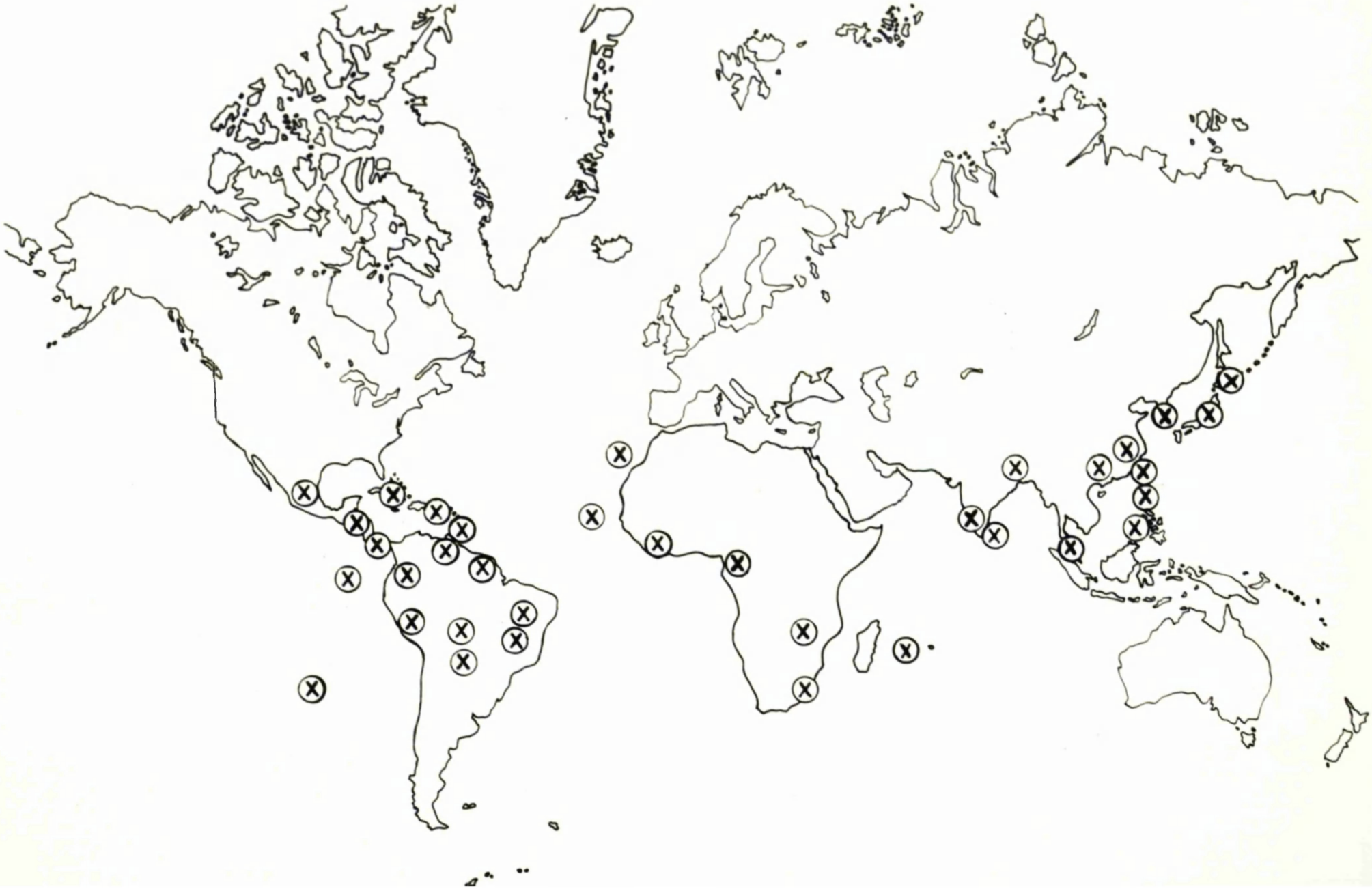
Notes on the anatomy of *Ophioglossum reticulatum* L. with special reference to its distribution in India.

INTRODUCTION

The Ophioglossaceae differ in several respects from all other groups of ferns. The characteristic features of these plants are the peculiar fertile spike, non-circinate vernation of the leaves which have stipulate sheaths, slow rate of growth and lack of well developed protecting and supporting tissues in the sporophyte. Unfortunately there are no fossil records of these plants, but they possess features which suggest that they are of great antiquity and that they represent a relatively primitive type amongst ferns. For example, the occasional dichotomous branching of the stem and root, dichotomous branching of the leaf-trace and vein endings, large sporangia with massive walls, vascular supply and stomata, no elaborate mechanism for dehiscence, and large spore output by individual sporangia: all are characters found in the primitive members of the Filicales. These unique plants with their peculiar fronds have attracted the attention of Pteridologists since the time of Rooper (1826) and have been repeatedly investigated and discussed.

The following account relates to *Ophioglossum reticulatum* L., with special reference to its geographical distribution and anatomy. The problem presented by the morphology of the fertile spike has also been re-examined. The earliest account of the anatomy of this species is that of Bower (1896), which deals in particular with the development of the sporangia and spores. Recently, in his studies on the Japanese species of the Ophioglossaceae, Nozu (1956) referred briefly to certain features of this species but Nishida (1957)

Distribution of Ophioglossum reticulatum in the World



has expressed doubts about the identity of the plants described by Nozu, considering that they might simply be a large type of O. vulgatum. No full account of the distribution and anatomy of O. reticulatum has hitherto been published.

DISTRIBUTION OF OPHIOGLOSSUM RETICULATUM

(a) World distribution

Ophioglossum reticulatum has been recorded from North Argentina, Bolivia, Peru, Brazil, Dutch Guinea, Venezuela, Colombia, Panama, Honduras, Guatemala, Costa Rica, Mexico (States of Jalisco, San Luis, Potosi, Vera Cruz), West Indies (Grenada, Hispaniola, Guadeloupe, Porto Rico, St. Thomas, Jamaica, Martinique, Isles of Cuba), Galapagos island (Villamil Mt.), Madeira, Cape Verde islands, Liberia, Cameroons, Nyassaland, Natal, Re Union, Mauritius, India, Burman, Nepal, Ceylon, Philippines (Island of Luzon, Province of Battan, Batangas, Benequet, Ilocos Norte), China, Korea, Japan, Formosa, Eastern Polynesia, Singapore.

The world distribution of this species shows that it is Gondwanic in distribution, and further emphasizes that this species is of great antiquity.

(b) Distribution in India

Ophioglossum reticulatum has been recorded from the following localities: Assam: Thakureswari or Monkey hills; Gauhati Grand Trunk Road, Goalpara Dist. (altitude about 200', collected by J. Marten, Nov. 1903); Khasi hills (collected by S. Bose, 1956). Bengal: Darjeeling (collected by U.L. Sen in 1958); Malda (Vicary, 1831); Agartalla (alt. 600 - 800' collected by P.M. Debbarman, April 1915); Indian

Botanic Gardon, Shibpore (collected by Davis, August 1896); Jadavpore (A.K. Ganguly, 1954). Bihar: Parasnath Hill (collected by J. Anderson at 3000', and also by the writer in Sept. 1958 at altitudes 3000 - 4,430'); Hazaribagh (near railway station by the writer in Sept. 1958). Bombay (now, Maharashtra): *Poona (T.S. Mahabale). Uttar Pradesh: Mussoori (collected by P.W. Mackinnon, Oct. 1883, and also by the writer in 1954); Dehra Doon (collected by M.B. Raizada, 1958). South India: North Canara (collected by Jalbot, July 1888); Mount Stuart, Annamalai Hills (altitude, 2,200', collected by Fischer in August 1905); Quilon; Travancore (collected by M.A. Lawson, Nov. 1895); Organ Mt. (Icllierst); Courtallum; *Bangalore (on the Nandai Hills, collected by T.S. Mahabale); Nilgiri Hills (Beddome). Kashmir (collected by T. Singh, 1957).

(All plants, excepting those marked with *, recorded above have been examined by the writer.)

MATERIAL

Material for anatomical studies was collected by the writer from the Parasnath Hills (in October, 1958) and also from Mussoorie (in November 1954). Material from Dehra Doon, collected and fixed by Dr. M.B. Raizada in October 1958, was sent to the writer for his studies. Material from Jadavpore, Kashmir, and Ceylon was available through the courtesy of the authorities of the City College, Calcutta, Mr. T. Singh, and the authorities of the Botanic Gardon, Ceylon, respectively.

The plants were collected, washed thoroughly and were immediately fixed in either of the two following fixatives for twelve hours.

a. 70% Alcohol ..... 1 part
Commercial Formalin 1 part
45% Acetic Acid ... 1 part

b. 10% Formalin ..... 3 parts
10% Acetic Acid ... 1 part
70% Alcohol ..... 6 parts

The material was then transferred into Acetic : Alcohol (1:3) for twelve hours and was then finally preserved in 70% Alcohol.

HABITAT IN INDIAN LOCALITIES

In India this species is found both on the hills as well as on the plains. The most luxuriant growth of this plant was recorded by the writer on the Parasnath Hills (altitude 4430 feet). The soil there is a stiff reddish loam with a high percentage of ferrous magnesium silicate. The maximum and the minimum rainfall occurs usually in the months of July and December respectively. From July to September the climate is warm and wet with a varying temperature of 22 - 25°C, while it is dry and comparatively cool from the middle of October to the middle of February, when the temperature often falls below 10°C. On this hill the plants were found in colonies in association with Selaginella (two species), Adiantum (one species) and grasses (three species), under the shade of stunted trees and shrubs, where these small ferns hardly got more than an hour's exposure of light in a day.

On the Mussoori Hill, the writer collected these plants at an altitude of 6000 feet during the month of October when there was heavy rainfall and the temperature was comparatively warm. Here the plants were found growing in association with two species of grass and under the shade of small bushes. It was gathered from the local people of both the above mentioned localities that this plant begins to perennate from early November when extreme cold sets in.

On the plains, some hundreds of miles away from hills this plant has been found, though not growing very luxuriantly, on moist, shady, grassy slopes during the rains. Often they have been found on dry open places, and even on roadsides during the same season.

In Bombay Presidency the plant has been reported to be growing under the thickets of Lantana camera, Caesalpinia pulcherrima, or near the trunks of Casuarina equisetifolia.

EXTERNAL CHARACTERS

The plants are herbaceous and perennial, varying from 4 to 40 cm in height according to the nature of the habitat. The plants growing on the hills in a warm and wet climate are usually larger than those growing on plains in hot and comparatively dry weather. A high water content of the soil also seems to promote the growth of this plant.

The stout, erect root-stock is more or less cylindrical and is glabrous throughout. It is usually unbranched but in rare examples, branching occurs as a result of the development of axillary buds. The pale brown root-stock shows spirally arranged leaf-scars near its base.

In the majority of plants available for examination there is a horizontal root present at the base of the plant. This is due to the fact that the vegetative propagation by adventitious root-borne buds is general, almost all the plants in a colony arising by this means. The basal horizontal root is thus a root of the parent plant. The roots developed by the new plant are usually inserted below the leaf-scars and grow obliquely downwards. These roots, which are devoid of root hairs, are mostly unbranched but a few of them show monopodial branching.

The erect fronds varying from 7 to 26 cm in length, the division into sterile and fertile regions occurring about

half-way up the frond. The sterile part consists of a short stalk (2-6 mm in length) bearing the undivided blade. The latter is membranous, glabrous, broadly ovate, or more or less cordate; the apex is rounded or obtuse; it measures 2-9 cm and 1.5-5 cm in breadth. The venation of the blade is reticulate and there is no distinct midrib. The veins form small polygonal areas varying from 0.4-12 mm in length and 0.4-3 mm in breadth. Veins within the areoles and others near the blade margin branch dichotomously and end blindly.

Under natural conditions usually only one frond is produced each year and this develops during the rainy season. On the Parasnath Hill, where the dry season begins in late October, the leaf dies down in late November and the plant becomes dormant. The new leaf begins to develop in early July.

Under cultivation, however, plants have been induced to produce up to three leaves in a single year before they became dormant. Ten plants, collected from Parasnath Hill on the 10th September, 1958 were planted in earthenware pots containing soil and humus from the same locality. The pots which were watered once in a week, were placed in a damp shady place, where sunlight was available for about one hour per day. The temperature ranged from 22 - 25°C. Seven plants either died or became dormant without producing further fronds during the year of the experiment. The remaining three behaved as follows:

Plant 1 - A new frond developed early in November. This was followed by the production of a second frond late in the following January and of a third frond (with spike) early in April.

Plant 2 - Development followed the same course as in plant 1. The first new frond was produced late in October, the second (bearing a spike) in the middle of the following

January and a third early in April.

Plant 3 - A new frond was produced in the middle of November and a second frond early in February. The plant then died.

It is clear therefore that the conditions of the experiment tended to retard the onset of dormancy and to stimulate the continued development of two or three young leaf rudiments already present at the apex.

During the experiment it may be noted that the intensity of habitat factors like temperature, daily exposure of sunlight (insolation), ground moisture, and atmospheric humidity was kept more or less similar to that available to the plant on the hill during the months of July to September, when the plants show active growth. It seems likely that if there had been no adverse environmental condition on the hill and elsewhere, the plants would have produced a new leaf at intervals of 2-3 months, and there would have been no period of dormancy. In other words it can be concluded from the above experiment that the monophyllous nature of the plant is an acquired character due to extreme specialization.

The fertile spike is borne about half-way along the length of the frond. It has a sterile stalk (peduncle) measuring 3-17 cm in length while the fertile region with its two rows of lateral sporangia measures 1.5-4 cm in length.

All the fronds produced by the plant do not bear a fertile spike. These sterile fronds, however, bear abortive spikes. Such abortive spikes are visible even on the leaves of very young plants, when they resemble the withered remnants of fertile spikes. Bower (1901) designated those leaves which bear undeveloped rudiments as sterile sporophylls and regarded the imperfect spikes as vestigial.

Ophioglossum reticulatum L.

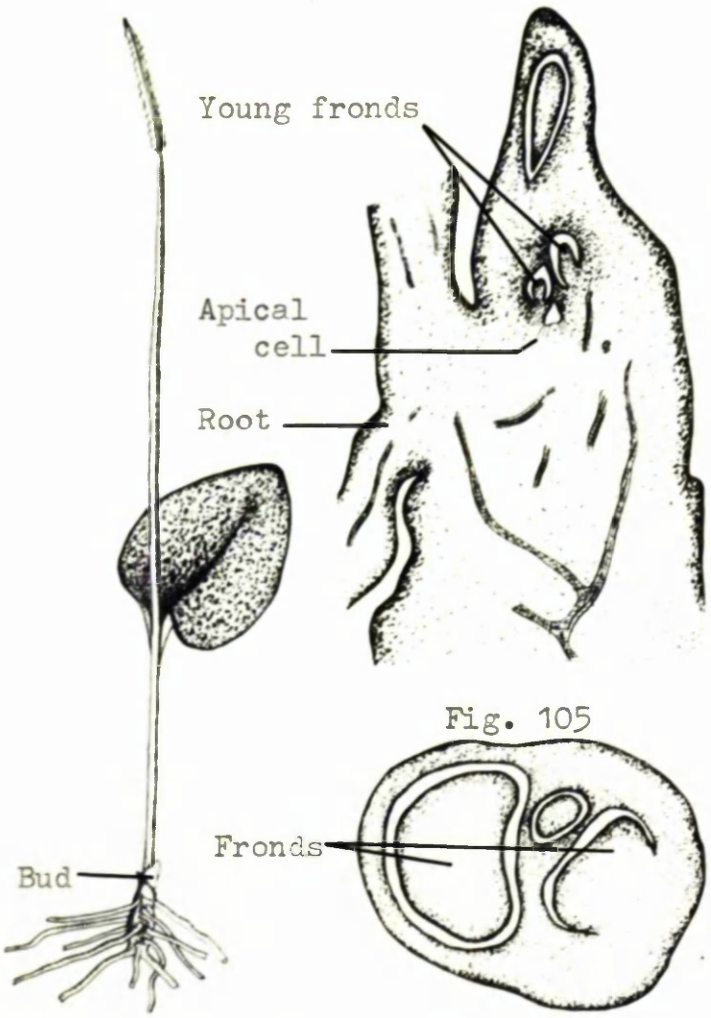


Fig. 104

Fig. 105

Fig. 106

Fig. 108

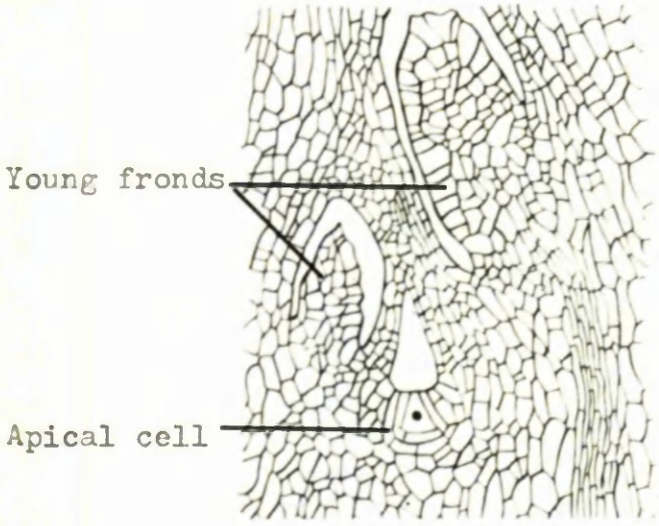


Fig. 107

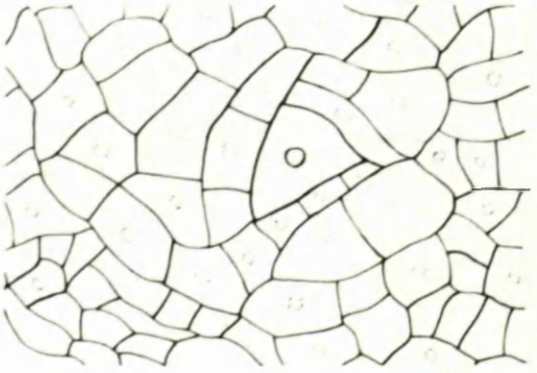


Fig. 109

Fig. 104. An adult plant. Fig. 105. L.S. of a stem. Fig. 106. T.S. of a stem near the apex. Fig. 107. L.S. of the stem showing the apical cell. Fig. 108. Vascular skeleton of a stem. Fig. 109. An apical cell of a root (T.S.). (104, x .5; 105, x 8; 106, x 20; 107, x 40; 108, x 7; 109, x 130.)

Ophioglossum reticulatum L.

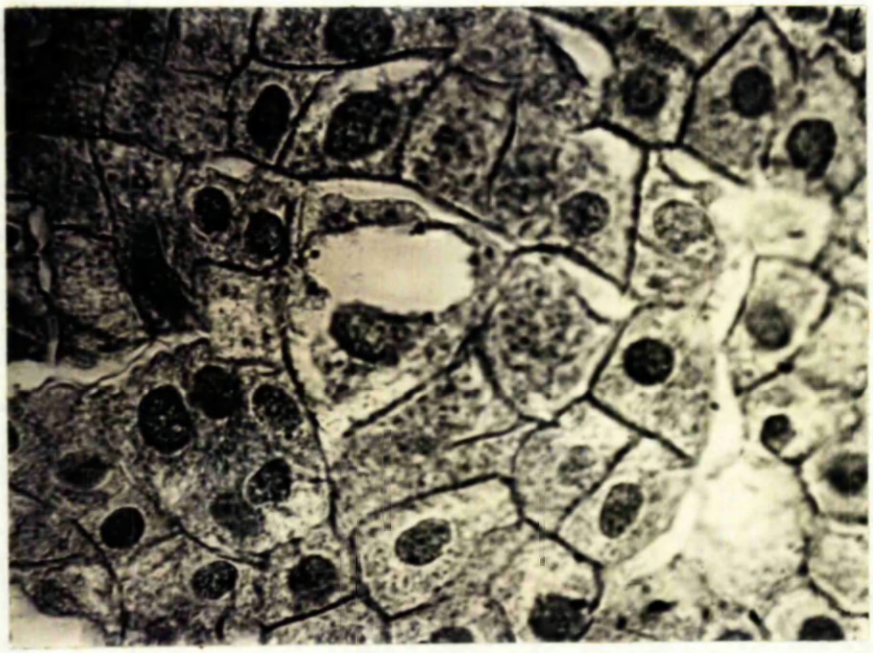


Fig. 110. An apical cell of a stem (T.S.). (x 270.)

THE STEM

(a) General description of apical region

The apical region of the root-stock is occupied by a bud (fig.104). Longitudinal and transverse sections through the bud (figs.105 and106) show that it consists of 3-6 spirally arranged rudimentary leaves of various ages. Each of these rudiments is surrounded by a stipular sheath formed by the base of the preceding leaf. A median longitudinal section of the bud shows that the apex of the root-stock lies in a small cavity formed by the overarching of the sheaths of the two youngest leaves (figs.105,107). This cavity opens to the exterior by a minute pore.

(b) The apical cell

The growth of the stem is due to the activity of a single truncated pyramidal apical cell which in longitudinal section is four-sided with a narrow apex and broader base (fig. 107), while in transverse section it is three sided (fig.110). After cutting off three lateral segments, either in a clockwise or anticlockwise direction, the apical cell cuts off the fourth segment from its basal side. The fifth and the sixth divisions are in a vertical plane in each of the lateral segments. Further divisions are in irregular sequence.

The apical region shows no sign of formation of cauline provascular tissue connecting either with the vascular system below the apical meristem or to that of the lateral appendages (fig.105). Mitosis in the cells of this region is not very frequent, indicating the very slow rate of growth of the stem.

(c) Short account of the general anatomy of root-stock

The root-stock is differentiated into epidermis, cortex and stele. The epidermis is single layered, thick walled

and consists of living cells. The cortex is composed of parenchymatous cells with intercellular spaces. These cells are packed with starch grains. An endodermis is present only in the basal region of the root-stock. The basal part of the root-stock shows an ontogenetic recapitulation of stelar evolution in being protostelic for the few nodes, ectophloic solenostelic for the next node and dictyostelic above this. Each meristele is endarch. Secondary growth is lacking.

(d) The vascular system

The general form of the vascular system in the stem of a young plant arising from a root is shown in fig. 108. The preparation upon which the drawing is based was obtained by using Sporne's rapid clearing technique. The root-stock was immersed in alkaline Hydrogen peroxide for about 48 hours and then heated in pure lactic acid for about four hours. This method, aided by careful dissection during the heating process, gives a clear picture of the entire vascular system, which is seen attached to the root strand of the parent plant. It remains unbranched for a short distance and then breaks up into a reticulum due to the overlapping of several leaf-gaps. The leaf-gaps are large, elongated and are arranged near the basal region in compact spirals. The leaf traces are clearly delimited from the cauline strand in the basal part of the root-stock while in the upper region this delimitation between the cauline and the foliar strands is not possible. In the lower region of the stem usually a single leaf-trace and a root-trace can be assigned to a single gap while in the upper region such assignment cannot be made. The leaf-traces remain unbranched till they emerge into the petiole. Some of the root-traces, specially those in the basal part, immediately after they are delimited from the cauline strand, pass upwards and outwards for a short distance and then bend down, while the others are directed downwards from the very

Ophioglossum reticulatum L.

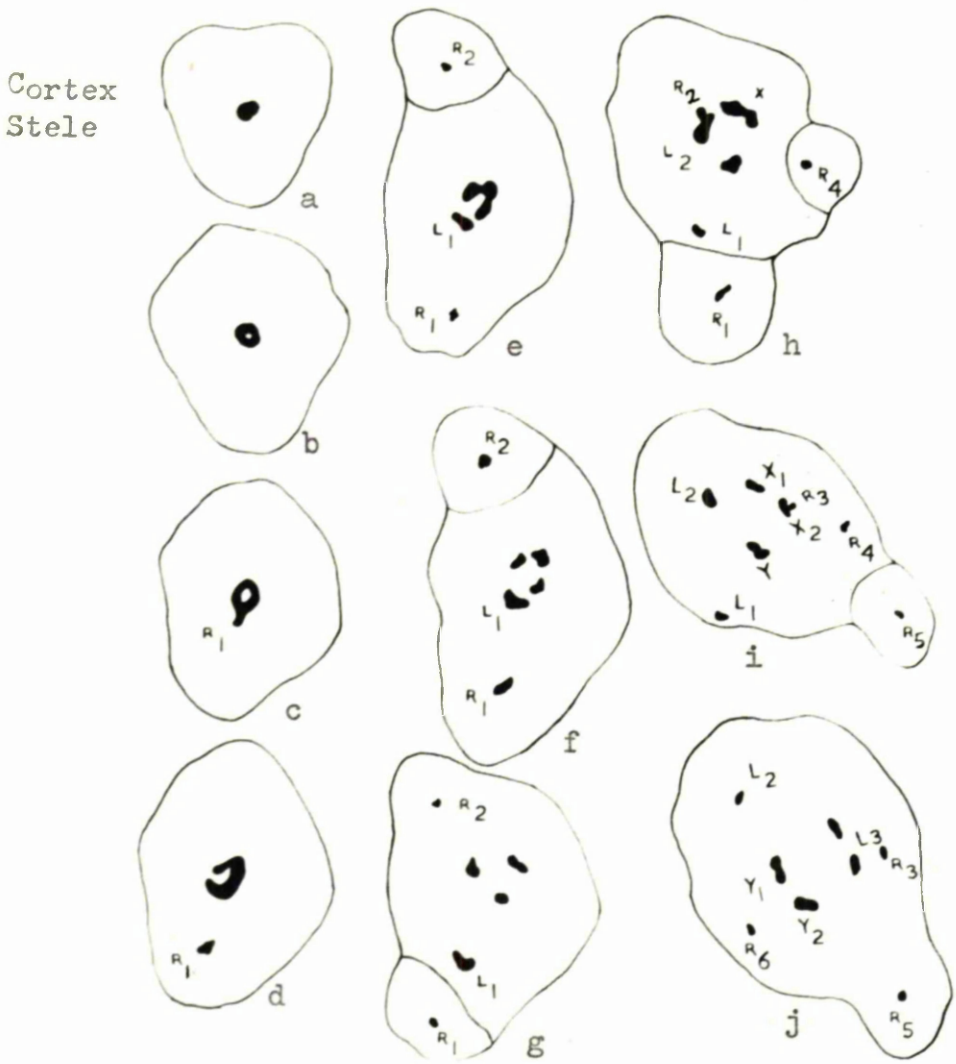


Fig. 111. Serial transverse sections of a stem showing progression from a protostelic to a dictyostelic condition (L_1, L_2, L_3, leaf-traces; R_1, R_2, etc., root-traces). (x 20.)

beginning.

(c) Description of transverse series

A transverse section at the basal part of the root-stock shows that in the centre the phloem surrounds the smooth core of the xylem to form a haplostelic structure (Fig. 111,a). Another section a few mm above the basal region, shows in the centre of the xylem the appearance of a parenchymatous mass, which becomes more conspicuous further up to form the siphonostelic structure (Figs. 111 ,b-c). Thus in this species, it is evident that the pith is intrastelar in origin. A similar section further up shows the vascular cylinder perforated by a leaf-gap to form a solenostele (Fig. 111 d). Further up, due to overlapping of several gaps, the vascular tissue breaks up into several meristeles to reach the dictyostelic condition (Fig. 111,f).

Figure 111,c shows a projection (R_I) from the outer surface of the stele. This projection is cut off at a higher level from the stele, passes upwards and outwards for a short distance and then bends back to form the root trace (figs. 111 ,d-h). Figures 111 ,e and f show that the stele breaks up into four strands, one of which passes upwards and outwards to supply the first leaf (L_I). Figure h shows the origin of another root trace as an outer projection of a strand. This trace, immediately after separation, goes down through the cortex and ultimately supplies the second root (R_2) (figs. 111 g,f, and e). In the succeeding sections it is found that after giving off the second root trace, the parent strand passes upwards and outwards, ultimately supplying the second leaf (L_2) (figs. 111 ,h-j).

The third root and leaf traces are found to develop in a similar way. Often a cauline strand is seen to bifurcate (e.g. X and Y in figs. h and i). Figs. 111,h-j show certain

root traces (R_4, R_5, and R_6), which have originated at higher levels, going downward and outward.

The leaf-trace therefore originates as a sector of the cauline strand. In many cases it is found that the size of a leaf-trace, as seen in a transverse section, is similar to that of a meristele. This similarity in size and the method of origin by dichotomization, is probably an indication of the morphological equivalence of the vascular axis in the stem and the frond. A similar type of leaf-trace formation was found in Botrychium by Chrysler (1945), who considered such a type of branching as dichotomous (dichotomy 1). As the leaf-trace ascends through the cortex, there appears a constriction near the middle of the inner side of its xylem mass. This constriction may be considered vestigial of the next dichotomy, and is similar to that of Ophioglossum nudicaule and O. kawamurae (Nishida, 1957). The constriction, however, is temporary and soon the leaf-trace regains its former shape, and becomes slightly curved. Immediately after entering the common-stalk, the curved leaf-trace divides into three by radial perpendicular divisions. The lateral strands occupy the adaxial position of the common-stalk, while the central one moves to the abaxial side (fig. 132). During this orientation of the strands, they rotate in such a way that their protoxylem points towards the centre. It is significant that the arrangement of these traces recalls that of the cauline strands.

(f) The xylem

The xylem is made up of tracheids and parenchyma, vessels being absent. The thickening of the walls of the protoxylem tracheids, as seen near the growing region, is annular. These tracheidal elements, as in the Marattiaceae, gradually grade into annular-reticulate elements. Tracheids with only

spiral thickening are not found, but reticulate-spiral elements are common in the metaxylem. However, a far greater number of the tracheids show scalariform-reticulate or reticulate thickening and have uniseriate or multiseriate, distinctly bordered, pits, which are more or less circular or elongated. Esau (1953) has also reported the presence of bordered pits in the protoxylem elements of the Ophioglossaceae, but Nozu (1956) could not recognise them in Japanese material, which also included Ophioglossum reticulatum. The tracheids of the metaxylem are about 0.4 mm in length and about 0.03 mm in breadth. By using stains like Tannic acid and iron alum with Safranin and Orange G, or, Haidenhains Iron-Hematoxylin and Safranin, it can be demonstrated that the tracheid walls are made up of three distinct layers, the primary, the secondary and the tertiary. It may be noted that this three layered condition was also observed by Loughridge (1932) in the tracheids of Ophioglossum vulgatum and Ophioglossum pendulum. The primary and also the secondary wall take cellulose stain, while the third layer takes the lignin stain. The wall of the mature tracheid with its tertiary deposition measures about 7.5 u in thickness, while its secondary thickening alone measures about 2.5 u. Sections through the pit-pairs show the presence of pit closing membranes similar to those of Ophioglossum vulgatum as shown by Wright (1920). The parenchyma associated with the tracheids are elongated cells and have their long axes parallel to those of the tracheids.

(g) The phloem

The phloem is composed of sieve cells and parenchyma. The sieve cells are arranged end to end with their end walls sharply inclined. The mature sieve cells as observed in longitudinal sections of the root-stock are enucleate, thick

walled and have sieve areas on all walls. These cells commonly vary in width, being either uniform throughout their whole length or narrower at one end. The wall consists of primary wall only, which stains as cellulose. The walls are thicker than those of the adjoining parenchyma cells and become considerably thickened at maturity. Callus could not be detected using anilin blue, zinc chloride, and iodine. A mature sieve cell has an average length of 0.175 mm and breadth of 0.01 mm. Often the thickening of the wall measures about 2 U. The parenchyma cells associated with the phloem are also elongated, having their long axes parallel to those of the sieve cells, and often show primary pit fields.

(h) The development of sieve cells

The development can be best studied at a distance back from the stem, root and spike apices. The very young sieve cells can rarely be distinguished from the other procambial cells. Like the procambial cells they are nucleate and vaculated. Gradually they become very much elongated and narrow. The nucleus also becomes elongated but finally disappears. Sieve areas can be seen in the developing sieve cells and these areas become increasingly conspicuous as the sieve cells mature. Starch grains, which are so abundant in the parenchyma cells, could not be detected in the sieve cells at any stage of development. No distinction could be made between the protophloem and metaphloem.

THE LEAF

(a) Development

Longitudinal and transverse sections of the root-stock reveal that three, four, five, or even six rudimentary leaves surround the apex. As a single leaf is usually produced by a plant in a year, it can be said that a leaf takes four, five,

Ophioglossum reticulatum L.

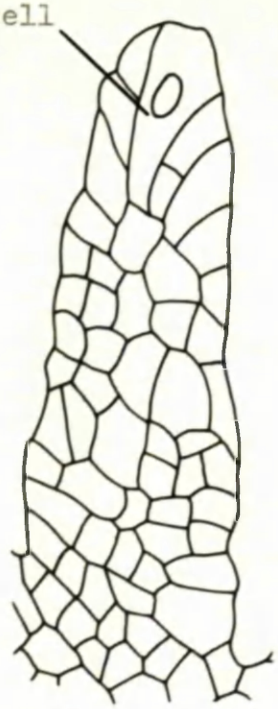


Fig. 112

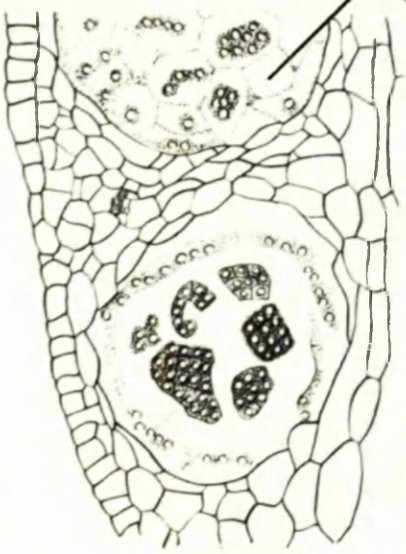


Fig. 116

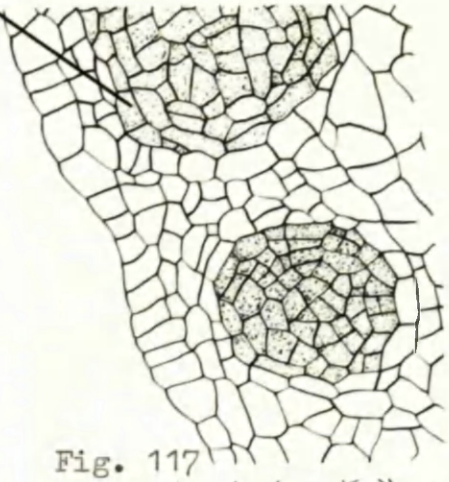


Fig. 117

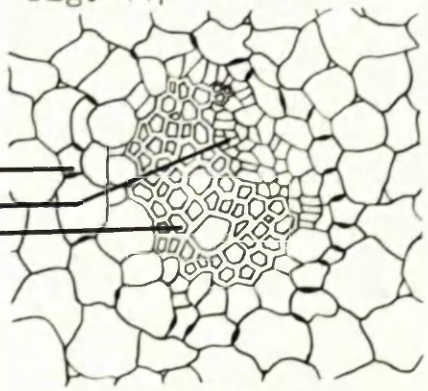


Fig. 120

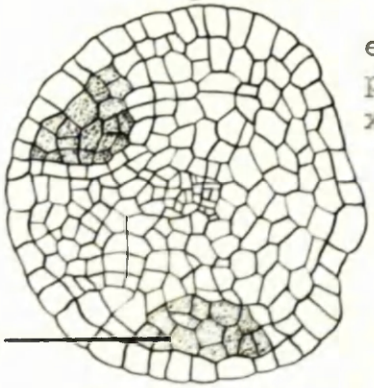


Fig 115

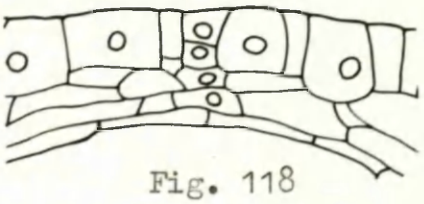


Fig. 118

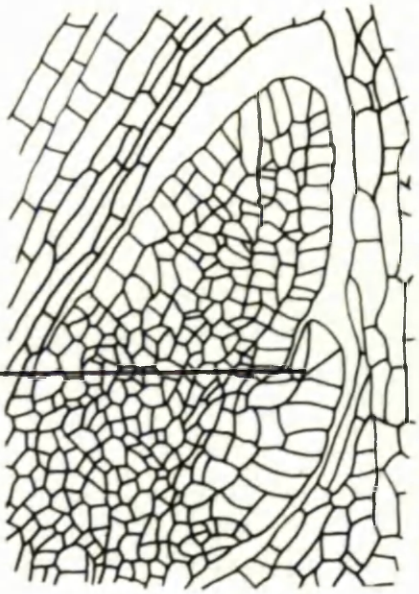


Fig. 113

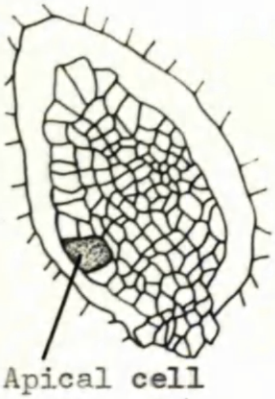


Fig. 114

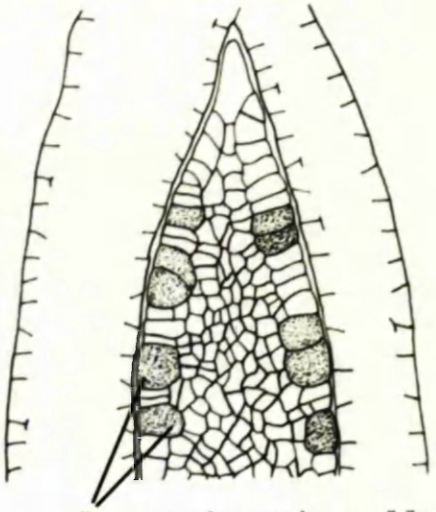


Fig. 119

Fig. 112. L.S. of a young frond. Fig. 113. L.S. of a young frond with a spike. Fig. 114. L.S. of a frond with an apical cell of the spike. Fig. 115. T.S. of of a spike. Fig. 116. L.S. of a part of a spike. Fig. 117. L.S. of a part of a spike. Fig. 118. T.S. of a wall of a sporangium showing the region of dehiscence. Fig. 119. L.S. of a spike. Fig. 120. T.S. of a root showing the endodermis (endo), phloem (ph), xylem (xy).

(112, x 62; 113, 114, 119, x 60; 115, x 105; 116, 117, x 48; 118, x 100; 120, x 75.)

Ophioglossum reticulatum L.

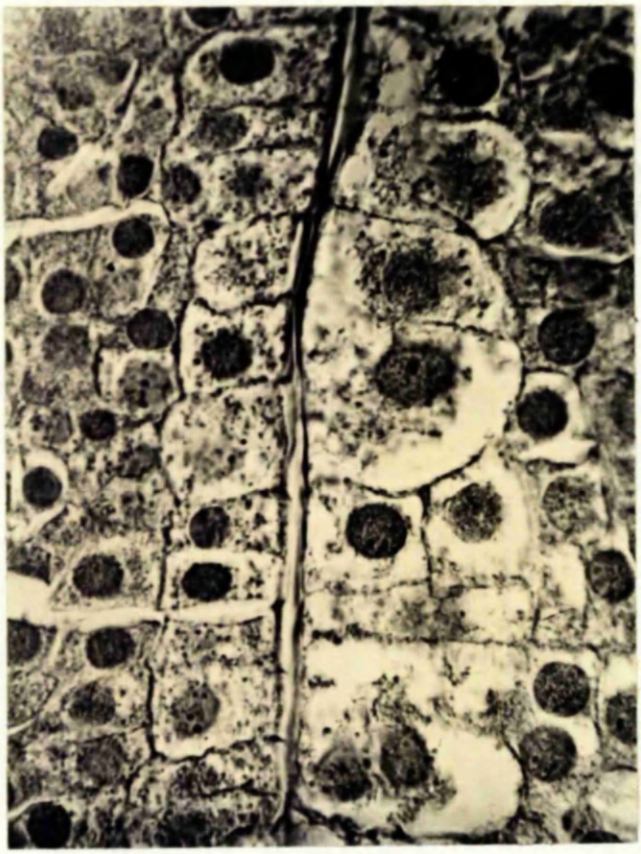


Fig. 120/A. L.S. of a young spike showing the sporangiogenic cells

(x 280.)

six, or even seven years to mature. A leaf develops by means of an apical cell having two cutting faces (fig.112). The leaf primordium is differentiated from one of the daughter segments of the apical cell of the root-stock. It consists of a conical mass of meristematic tissue which increases in size during the first two or three years of its development but does not show any differentiation beyond the formation of the spike initial (fig.113). Procambial strands then appear at the base of the rudiment and vascular tissue is fully differentiated in the leaf itself about two years before the leaf expands.

The cells of the meristematic tissue derived from the activity of the leaf primordium become active before the year of unfolding. In the region above the point of attachment of the spike, the meristematic tissue differentiates the marginal meristems, where more walls are formed by dividing cells anticlinally than periclinally. As a result a flat tissue or lamina is formed. At the time of unfolding, each leaf breaks through the stipular sheath of the preceding leaf, as in the other species of the genus.

(b) Anatomy of the common stalk

A cleared common stalk shows that the three traces at its base undergo repeated divisions as they pass upwards and form twelve traces at the level where the common stalk divides into the fertile and sterile lobes (fig.128). Of these twelve bundles, nine supply the sterile part, and the remaining three pass into the fertile lobe. In the common-stalk there is no sign of anastomosis among the traces. Serial transverse sections of the common-stalk confirm the above description. Figure 132 , which represents a transverse section of the stem-apex surrounded by a number of common-stalk bases, shows the division of the single leaf-trace into three. Just below the

Ophioglossum reticulatum L.

Fig. 121

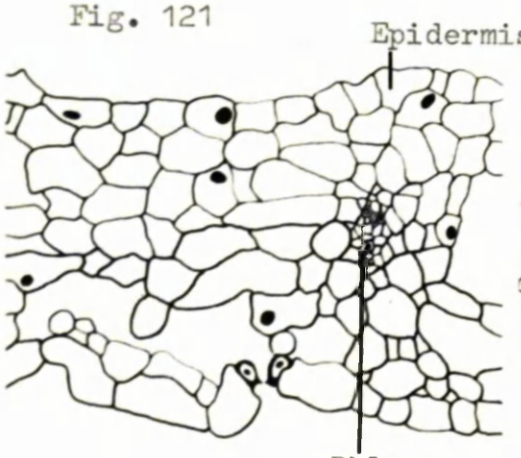


Fig. 122

Fig. 123

Fig. 124

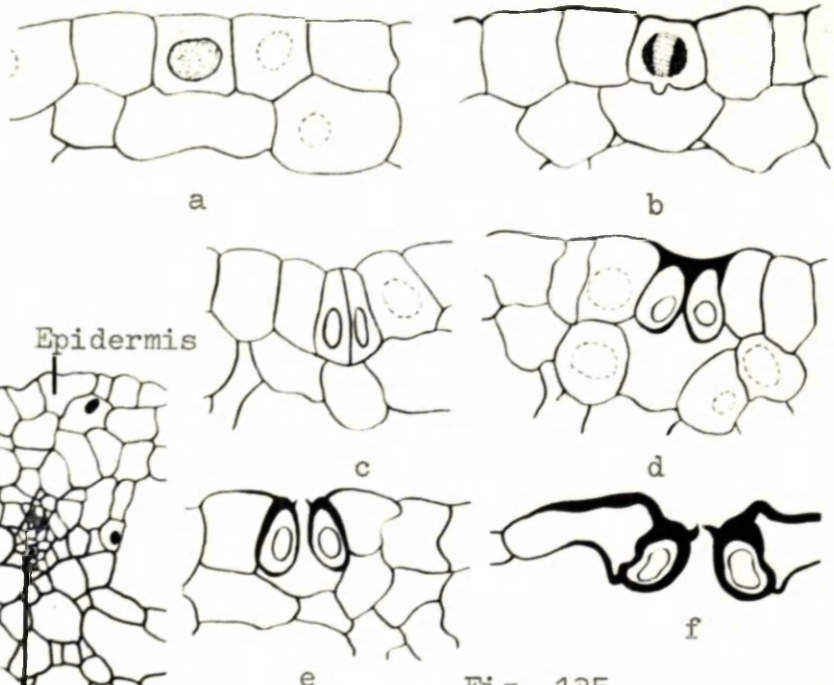


Fig. 125

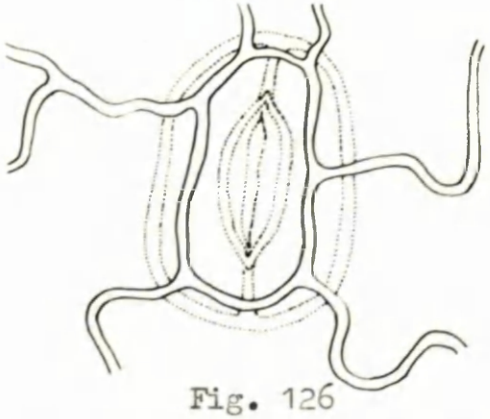


Fig. 126

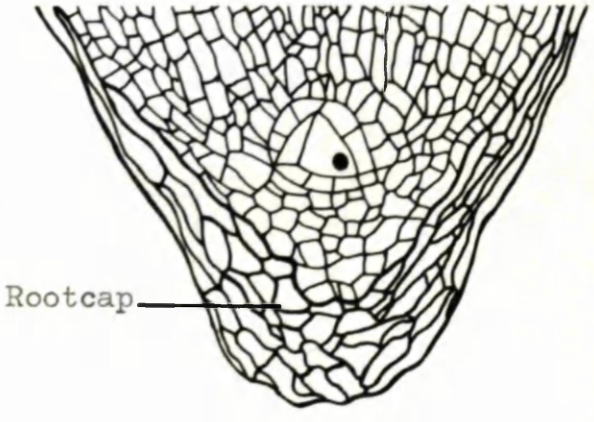


Fig. 127

Fig. 121. Epidermis of the common stalk showing a sunken stoma. Fig. 122. T.S. of a part of lamina. Fig. 123. Part of a lamina showing reticulate venation. Fig. 124. Epidermis overlying the veins. Fig. 125, a-f. Stomata in the stages of development. Fig. 126. A mature stoma. Fig. 127. L.S. of a root-tip. (121, x 42; 122, x 150; 123, x 9; 124, x 50; 125, 126, x 275; 127, x 115.)

Ophioglossum reticulatum L.

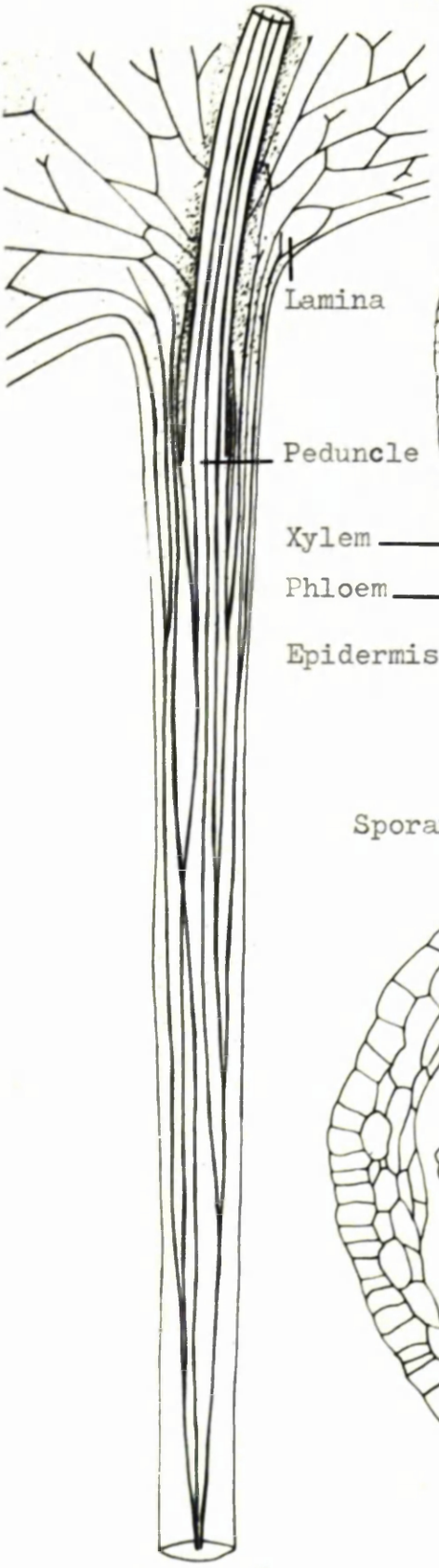


Fig. 128

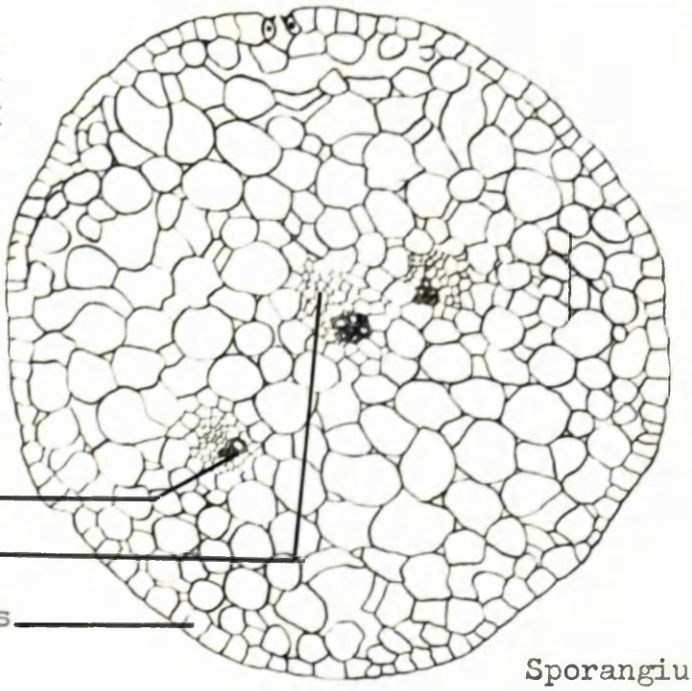


Fig. 131

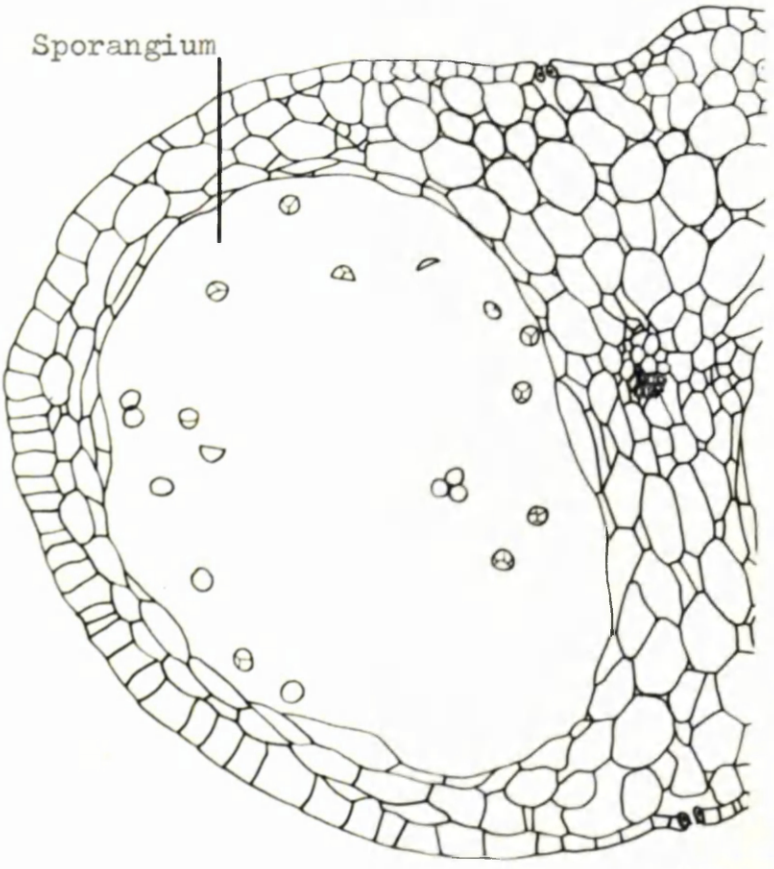


Fig. 130

Fig. 129

Fig. 128. A part of a frond showing dichotomous branching of the vascular strands. Fig. 129. A fertile spike, showing vascular supply to sporangia. Fig. 130. T.S. of a sporangium. Fig. 131. T.S. of a peduncle. (128, x 5; 129, x 9; 130, x 60; 131, x 65.)

Ophioglossum reticulatum L.

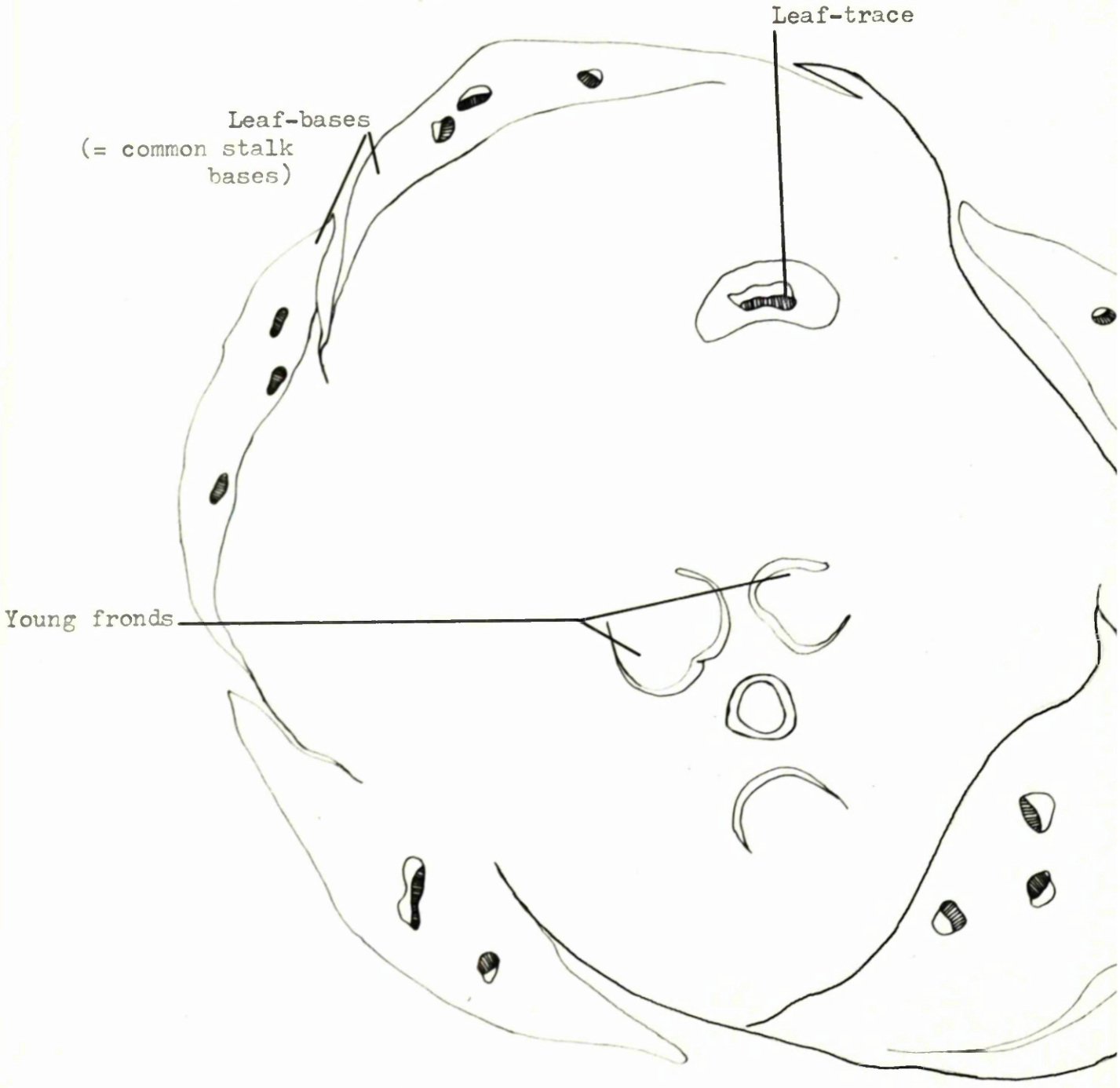
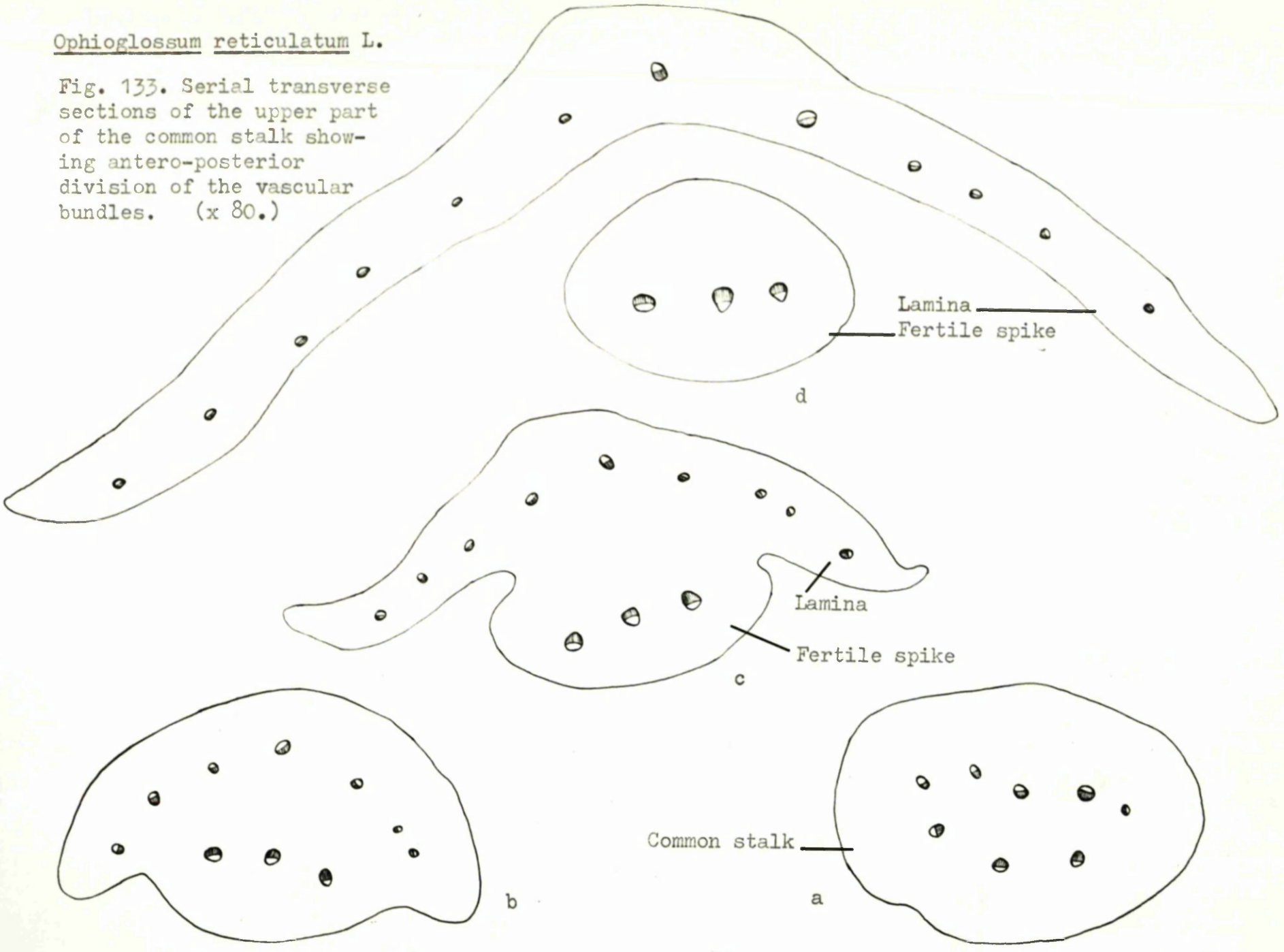


Fig. 132. Transverse section of a stem apex showing the common stalk bases. (x 80.)

Ophioglossum reticulatum L.

Fig. 133. Serial transverse sections of the upper part of the common stalk showing antero-posterior division of the vascular bundles. (x 80.)



Ophioglossum reticulatum L.

a

b

Fig. 134. Photograph showing the differentiation of veins at two different levels.

(x 10.)

external division of the frond into the sterile and fertile segments (fig.133 ,a) there is a ring of collateral strands. Figures 133 b,c and d, cut at successively higher levels, show the departure of three of the adaxial bundles to supply the fertile segment.

The xylem and the phloem elements of the vascular strands were examined in serial longitudinal sections. The protoxylem consists of tracheids with helical thickening and measuring about 0.3 mm in length and 0.01 mm in breadth. The metaxylem tracheids usually have uniseriate pitting, the pits being rounded to oval; they measure 0.3 mm in length and 0.02 in breadth. The sieve cells, which are very similar to those of the stem are usually about 0.4 mm long and 0.01 mm broad.

The epidermal cells of the common stalk are much elongated and have extremely oblique end walls. The sunken stomata are distributed over the entire surface. They resemble the stomata of the sterile blade in structure (fig. 121) and also in development.

(c) Venation

The reticulate venation of the blade is well shown in cleared specimens (figs.128 and 123). Free vein endings are present in some of the vein islets and they are particularly frequent round the margin. In a few abnormal cases veins have been differentiated at two different levels. Fig. 134 illustrates one such example where vein a is at a lower level than vein b.

(d) General anatomy of the lamina in transverse section

A cross section shows that the outer walls of the epidermis are cutinised and that sunken stomata are present on both the surfaces. The mesophyll cells are not differentiated (fig.122). They are irregular in outline, some of them being oval, others circular, angular and elongated. These

cells contain several disc-shaped chloroplasts, which are characterised by having dentate margins. Large air chambers are often found in the mesophyll between the traces. The traces have protoxylem facing the adaxial side and phloem the abaxial face. The xylem and phloem elements resemble those of common stalk.

(c) Epidermis and stomata

The epidermal cells on both surfaces of the blade have wavy anticlinal walls. Stomata are present in equal numbers on the two surfaces and they occur both over the veins and over the intervening mesophyll. The oval stomata, which are usually situated a little below the general level of the epidermis, have no subsidiary cells (fig. 126). The walls of the guard cells are unevenly thickened and there are ledges of cutinised wall material, appearing as horns in a section (fig. 125,f), projecting over the external opening of the stomatal pore.

The differentiation of the stomata was followed in sections of sterile blades of varying age. The stoma mother cells are readily distinguishable since they have denser protoplasts and larger nuclei than the neighbouring cells (fig. 125,a). The mother cell then divides by an anticlinal wall to give the two guard cells (figs. 125 ,b and c). The walls of these now become differentially thickened and cutinised, the outer walls being the most strongly thickened (fig. 125,d). Following the dissolution of the intercellular material between them, the two guard cells separate to form the stomatal pore (fig. 125,e). During the developmental stages the guard cells are at the same level as the general epidermis. As maturity is reached adjustments in the surrounding tissues lead to the stoma being sunk below the general epidermal level. There does not appear to be any

definite sequence in the development of stomata on a young leaf and frequently various developmental stages can be observed near to mature stomata.

ROOT

(a) Development

The growth of the root is due to the activity of a pyramidal apical cell having four cutting faces. In longitudinal section, the apical cell, which lies at a distance of about 0.3 mm from the root tip, shows that the segments derived from the side facing the root tip form the root cap by further divisions (fig. 127). The differentiation of the meristematic tissue into protoderm, ground meristem, and procambium within 0.01 mm from the apical cell was found in four roots. A median longitudinal section through the apical cell shows that it cuts off segments more or less regularly like that of a leptosporangiate fern. The first division, as is seen in a transverse section (fig. 109) is always periclinal. The second division is anticlinal, while the third division is usually anticlincal but in some cases it was found to be periclinal. The next divisions are in any plane. In the protoderm the cell divisions are always anticlinal. In the ground meristem the cells divide in all directions. In the procambial strand, cell elongation is rather more conspicuous than cell division.

(b) Transverse section of the root

The outer wall of theepidermis is suberised. The outer cortex which is about 0.25 mm in thickness and 3-7 cells across consists of angular cells without intercellular spaces. These cells contain endotropic mycorrhiza. In many cells much branched non-septate coenocytic hyphae are found, while in others irregular clumps of various sizes of the digested hyphae are seen. Few cells in the outer cortex are uninfected.

The inner cortex which is about 0.3 mm in thickness is composed of oval cells with intercellular spaces.

The cells of the inner and the outer cortex are packed with starch grains. The grains of the inner cortex are much larger than those in the outer one. The inner limit of the cortex is a clearly defined endodermis of primary type. The suberised bands of the endodermal cells, which are not clearly visible by ordinary stains, are readily demonstrated by staining with Ammoniacal Basic Fuchsin.

The solid xylem strand, roughly crescentic in section, is monarch (fig. 120), or diarch and occupies an average area of about 0.175 x 0.087 mm. Phloem elements, arranged radially, extend over its concave side. The protoxylem is composed of tracheids with annular-helical thickening. The metaxylem consists of tracheids with uniseriate or multiseriate torusless bordered pits. These tracheids vary from 0.18 - 0.22 mm in length and 0.01 - 0.04 mm in breadth. Their walls with tertiary thickening measure about 5 u while the secondary thickening alone measures about 2.5 u. The sieve cells, which are very similar to those of the stem vary from 0.15 mm to 0.228 mm in length and 0.014 - 0.25 mm in breadth.

THE SPIKE

(a) Development

The spike develops by the activity of an apical cell having four cutting faces. This apical cell has its origin from a superficial cell of a young leaf about one year old. When a young leaf attains a height of about 0.5 mm, a cell occupying a median position on the adaxial surface becomes differentiated (fig. 114). This cell, as it attains a diameter of about 0.035 mm and accumulates a dense protoplast, begins to divide to form a conical body of meristematic tissue. This conical body with its pointed tip turns upwards and grows

in the same direction as the young leaf (fig. 113), but it does not overtop the latter until the blade has unfolded. There is practically no differentiation of the cells in a young spike, but when it has attained a height of about 0.08 mm and breadth of 0.3 mm, some of the epidermal cells become conspicuous (fig. 120/A). These epidermal cells, arranged vertically along the two lateral margins of the flattened spike, become larger, often attaining a diameter of about 60 u (fig. 119). These larger cells with their differentiated protoplasts may be called 'sporangiogenic cells' as they later divide and redivide, ultimately giving sporogenous groups and the cells of the outer sporangial walls. These groups form a line down each side of the young spike but do not form continuous strips and are in fact separated by undifferentiated blocks of epidermal cells. Bower (1896) has described a sporangiogenic band consisting of a continuous ribbon of enlarged cells, the ribbon being two to three cells broad. Such a complete band does not occur in the plants of the localities examined by the writer. Thus the groups of the sporangiogenic cells are interrupted by undifferentiated blocks of epidermal cells, from the very beginning. In the next stage of development both the sporangiogenic cells and the undifferentiated cells undergo repeated division. The daughter cells of the sporangiogenic cells occupying the peripheral position contribute to the outer wall of the sporangium, while those occupying the centre develop into sporogenous cells (fig. 115). The epidermal cells and the ground tissue between the groups of sporangiogenic cells divide and redivide to separate vertically one sporangium from the other (fig. 117). At a stage when the sporangia are first formed, the central cells of the spike undergo differentiation to form procambial tissue.

(b) General structure

The vascular system of a mature spike is shown in the cleared specimen depicted in figure 129. As described above, three vascular strands enter the base of the peduncle. These divide at higher levels and six strands are present immediately below the sporangial region. These strands anastomose at intervals in the central axis of the sporangial region and there is a reduction in the number of strands from four at the base to a single one in the distal region. Small vascular strands extend horizontally from the axial system into the sterile tissue between the sporangia. Their tips are sharply recurved towards the sporangium below, and frequently branch into two or three. Cleared material dissected under a binocular microscope shows that in each case one of these ultimate branches supplies the sporangial wall while the other strand or strands end blindly in the abaxial tissue.

(c) Structure of the stalk

The anatomical features of the stalk are shown in fig. 131. There is a small-celled epidermis with slightly sunken stomata. The vascular strands are embedded in the entirely parenchymatous ground tissue.

(d) The sporangia and the spores

The large oval sporangia are laterally fused and each is supplied with a vascular trace. The individual sporangia measure about 0.5 - 1 mm in diameter, and have a jacket 3-6 cells in thickness. The outer layer of the jacket is composed of radially elongated large cells. Towards the side of the sporangium, these radially elongated cells become smaller and are the same size as the epidermal cells of the sterile region (fig. 130).

The very numerous spores are more or less yellowish to

light brown in colour when seen in masses. The spores are generally circular in outline. The muri on the exine are of uniform height (about 1 u), and have a notched outline. They form a continuous reticulum of more or less uniform meshes. Lumina of the reticulum are about 2 u in diameter. The meshes are polygonal. The rays of the trilete mark reach about 2/3 of the spore radius. They are more or less wavy, and not tapering. The contact-area is slightly prominent. The mature spores vary from 38 - 45 u in diameter.

The tapetum is two cells in thickness and is developed from the outermost layers of the sporogenous tissue. Burlingame (1907) has mentioned similar results in his studies on this species. The tapetum breaks down after the final division of the sporogenous tissue (fig. 116).

(e) Dehiscence

It has been noted that the outer layer of the jacket of the sporangium is composed of radially elongated cells. All cells of this layer are, however, not radially elongated, certain cells remaining small even at maturity (fig. 118). When the spores in a sporangium are mature these small cells separate allowing the spores to disperse.

Discussion and Summary

(a). Ophioglossum reticulatum, a distinct species from O. vulgatum

Since the time of Beddome (1892) attention has often been drawn to the morphological similarities between Ophioglossum reticulatum and Ophioglossum vulgatum. d'Almeida (1922) considered that these two species are merely forms of the same species, being connected by a number of transitional stages. Both the species have reticulate veins, and often the cordate, membranous frond of O. reticulatum approaches very closely the fleshy ovate frond of O. vulgatum. The two species can, however, be separated on the basis of their spore characters. The spores of O. reticulatum are reticulately ornamented, but although certain workers (Knox, 1951, and Nishida, 1959) have described the exospores of O. vulgatum as reticulately ornamented, a real reticulum is absent in this species. Here the ornamentation consists of verrucae of very variable size and shape. These verrucae are often laterally fused to form crested ridges. In polar view, on the surface, they produce a very irregular false reticulum, because of the coalescence of verrucae.

(b). Anatomy of the rhizome of O. reticulatum

Campbell (1911) in his account of the Eusporangiatae, concluded that the young rhizome of both the Ophioglossaceae and the Marattiaceae has no cauline vascular tissue and that the stem is made up entirely of the bases of leaves. A similar interpretation has been given by Maheshvari and Singh (1934) for O. fibrosum. Chrysler (1941) reported the presence of a solenostele in O. engelmanni, but stated that it is possible to interpret the vascular system of the rhizome of

O. palmatum as a congeries of leaf-traces. In O. reticulatum, however, both conditions are present. The basal part shows a definite cauline stele (Haplo- to Dictyostele), while in the upper part it is impossible to distinguish the cauline from the foliar strands.

(c) Leaf-trace

A double leaf-trace has been reported in certain species of Ophioglossum by Vasisht (1927), Maheshwari and Singh (1934), but, as in O. nudicaule, O. kawamurae (Nishida, 1957), a single leaf-trace is always found in both the young and the adult plants of O. reticulatum. Single leaf-trace formation is a characteristic of the primitive forms.

(d) Root

Campbell (1911) reported that almost all the species of the section Eu-Ophioglossum have monarch roots. Vasisht (1927), however, found di- to tetrarch roots in O. fibrosum. Maheshwari and Singh (1934) found diarch roots in O. vulgatum, and monarch to triarch roots in O. fibrosum. In O. reticulatum, though the monarch condition is predominant, a diarch condition is not uncommon, but none of the roots investigated showed a triarch condition. The variation in the number of the protoxylem groups may be correlated with the size of the root.

(e) Fertile spike

The morphological nature of the fertile spike has been the subject of much discussion and various interpretations of this characteristic structure have been put forward.

Roeper (1826) was probably the first to suggest that the frond in Botrychium represents a pair of leaves - one fertile and one sterile, with their petioles fused together. Braun (1838) suggested that the spike represents the only developed leaf of a bud seated in the axil of a sterile frond. Presl

(1845) and Mettenius (1856) however suggested that the fertile and sterile parts of the frond are segments of the same leaf. In 1859, Roeper relinquished his former view and stated that the fertile spike in Botrychium represents two lateral basal pinnae of a frond, the remainder of which is sterile. Holle (1875) extended this view to Ophioglossum and drew a comparison with the condition found in Anemia. Goebel (1884) suggested that the fertile spike is the lowest pinna of the sterile frond and that it arises not laterally but in a median position.

Bower (1896) made a completely different proposition and suggested that the spike should be regarded as the homologue of the sporangium of a lycopod. Campbell (1890) also gave a very different view, and derived the fertile spike of Ophioglossum directly from the sporangium of Anthoceros.

Chrysler (1911) studied the anatomical details of the frond of Botrychium and found that the crescent shaped leaf-trace as it ascends the common-stalk divides into two. From the lateral margins of these two strands, two other smaller strands are cut off. These smaller strands pass up the peduncle and each one supplies the lobes and sporangia of its side. Above the region of attachment of the fertile spike, two lateral strands are formed in a similar way, and each of them supplies a single pinna. Chrysler concluded that these anatomical details lend support to Roeper's view that the fertile spike represents two fused pinnae.

Bower (1911) also concluded that in accordance with the anatomical facts, the spike should be held to be ultimately of pinna nature, in most cases being the result of pinna-fusion, but this unit is subject to repetition in O. palmatum. This view was maintained in Vol. II of The Ferns (1926).

Increasing knowledge of early vascular plants, such as the Psilophytales, led to a re-examination of the problem

presented by the fronds of the Ophioglossaceae. Zimmermann (1930) interpreted them on the basis of his telome theory as being derived from the shoots of primitive land plants such as the Psilophytales or the Coenopteridales. Bower (1935), after stating that the interpretation of the spikes as being of pinna origin had never been fully convincing, adopted the view that they 'are best ranked among parts of indeterminate origin, such as many of the earlier vascular fossils present'. He thought that the spike and sterile blade could be regarded as resulting from an antero-posterior dichotomy.

Later work has supported the view that the fronds represent a condensed dichotomous branch system. Chrysler (1945), who studied the dichotomous branchings of the leaf-trace of Botrychium, stated that it is possible to interpret the frond in the light of the telome theory. Nozu (1950) and Nishida (1957) concluded that the common stalk is a stem-like organ and termed it a phyllomophore.

The facts described above relating to the anatomy and development of the frond of O. reticulatum support, in certain points, the view that it may have been derived from a much modified and condensed dichotomous branch system. Salient features are:

1. The leaf-trace and venation clearly show a series of dichotomous branchings. By the first dichotomy the leaf-trace separated out from the cauline strand. The next dichotomy is rudimentary, while by the third dichotomy, the leaf-trace produces three strands, which by similar divisions form about twelve bundles. These bundles are arranged in such a way that the common-stalk suggests a stem structure. This soon undergoes an antero-posterior division. The bundles of the fertile half undergo repeated divisions and fusions as they ascend.

2. Developmental studies suggest that the spike and the sterile blade are formed by an antero-posterior dichotomy.

3. The sporangia arise at the tips of ultimate branchings.

4. The 'petiole' or common stalk shows a stem-like anatomy.

On the other hand, the frond certainly approaches the structure of a modern fern frond in other respects. The fronds, at least in the basal part of the rhizome, are spirally arranged and are associated with gaps in the vascular cylinder. The anatomy of the sterile blade is entirely leaf-like. A further leaf-like feature is the development of axillary buds and branches.

Hence, considering all these facts, it seems reasonable to conclude that the frond of Ophioglossum is an organ intermediate between a true leaf and a branch.

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